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OÖSORPTION AND OVULATION IN RELATION TO OVIPOSITION IN THE PARASITIC HYMENOPTERA[1]

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In the parasitic Hymenoptera the gravid female deposits few, if any, eggs except in response to a certain complex or chain of stimuli which are host-connected. When conditions are favorable for oviposition, the number of eggs that each species places on each individual host is fairly constant and is largely independent of host density; this in spite of the fact that in gravid females oögenesis, if not complete before emergence, may be continuous and proceeding at a constant rate.

The apparent restraint in oviposition on the part of the searching female insures the reproduction of the species when hosts are scarce. The isolated host, discovered after prolonged searching, usually receives the normal number of viable eggs, that is, the number that can develop and emerge from one host individual.

The morphological and physiological conditions in the female which may govern this selective action are outlined in this presentation.

It is convenient to classify the eggs of the parasitic Hymenoptera on the basis of the utilization of the embryonic membrane in obtaining nourishment from the host's fluids; a phenomenon herein designated *hydropy*. Eggs in which the embryonic membrane becomes xenotrophic in function are *hydropic;* eggs in which the embryonic membrane does not assume this function are *anhydropic*. See plate I, figs. 1 and 2.

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Hydropic eggs (plate I, fig. 1) may be deficient in yolk or almost devoid of it (alecithal). The growth of the trophic membrane causes the egg to increase enormously in size (Jackson, 1928). In some species the egg hatches precociously, that is, when the embryo is in the protopod stage of development (Imms, 1937). Hydropy has been observed in many species of endoparasitic Hymenoptera since Henneguy (1892) noted it in *Smicra clavipes*. It is noteworthy that hydropy is a prerequisite of polyembryony.

In anhydropic species there is no discontinuity in the development of the egg and embryo if conditions are favorable for the deposition of all ripe eggs; consequently the ovulated egg must be deposited before it hatches. Since the germarium as a rule is not depleted of oögonia before the death of the female, the number of eggs available at any time for deposition is fairly constant.

TABLE I

EXAMPLES OF HYDROPIC AND ANHYDROPIC SPECIES

Family	Hydropic Species	Anhydropic Species[5]
Chalcidoidea[3]....	*Quaylea whittieri* (Gir.)	*Metaphycus lounsburyi* (How.)
	Coccophagus capensis Comp. (female)	*Coccophagus capensis* Comp. (male)
Ichneumonoidea.	*Therion morio* F.	*Pimpla instigator* F.
	Apanteles glomeratus (L.)	*Microbracon brevicornis* Wesm.
Serphoidea[4].....	*Scelio pembertoni* Timb.	*Lygocerus niger* How.
Cynipoidea[4].....	*Ibalia leucospoides* Hoch.	

[3]Species observed by the writer.
[4]The embryo may hatch when in the protopod stage of development in certain hydropic species.
[5]The anhydropic group includes many endoparasitic species. In *Coccophagus ochraceus* the fertilized egg develops endoparasitically and the unfertilized egg ectoparasitically on lecaniine scale insects.

In hydropic species the eggs are comparatively small. Ripe eggs may be stored pending their deposition in the paired oviducts and in the basal portion of the ovary. In some species the germarium may be depleted of oögonia either before or soon after the female emerges, ovulation occurring as rapidly as the eggs become ripe. In such species the oviducts are adapted for the storing of a large number of eggs.

It is obvious that the apparent restraint in oviposition in many hydropic species is dependent in part at least on the capacity for the storing of ripe eggs. This storage capacity is

very limited or lacking in anhydropic species, yet they also exhibit restraint in oviposition. It seems that this ability in species that lack storage capacity is an effect of the sorption of the ripe egg while it is enclosed in its follicular membrane. When hosts are lacking, oösorption occurs at the same rate as oögenesis. Ovulation in anhydropic species is dependent on an external stimulus and precludes oösorption only when conditions are favorable for oviposition. This is the case also in hydropic species that lack the capacity for storing eggs.

OÖGENESIS

Oögenesis in the Hymenoptera proceeds in the ovariole in a line comparable to line production in modern industrial operations. The material used in the fabrication of the ovarian egg consists largely of the nitrogenous food consumed by the female during its larval or adult life. In many of the anhydropic species the food consumed and stored during the larval period is insufficient for the development of its supply of oögonia. The adult female of such species habitually feeds on the body fluids of its developmental host. This habit, according to Clausen (1940), is known to occur in species representing about 25 families of parasitic Hymenoptera. It seems to be absent in hydropic species.

In some species, as in the pteromalids, *Spintherus*, *Dibrachoides*, and *Peridesmia*, parasitic on the alfalfa weevil, *Hypera postica* (Gyll.), host feeding by the newly emerged adults must precede oviposition. In a large number of host-feeding species, however, the female, as in *Metaphycus helvolus*, is able to deposit a few eggs before commencing to feed on host fluids. Host-feeding females as well as many non-host-feeding females require carbohydrates, such as honey, nectar, or honeydew, for total oviposition.

In the absence of hosts, the females of species in which oögenesis is dependent, entirely or in part, on host-feeding during the adult stage, appear to have fewer ripe eggs in the ovaries at a time and to be longer-lived than those in which complete oögenesis is independent of such host-feeding.

Oögenesis in many, if not most, anhydropic species of Hymenoptera may proceed without interruption until the death of the female. The habit of the adult female of feeding on nitrogenous food, however, is correlated, in some species, with the *temporary* cessation of oögenesis, which may occur either spontaneously or as a result of environmental conditions.

In such cases, oögenesis may either stop or start through the influence of other factors. In the social wasps, Marchal (1896) observed that workers became fertile merely as the result of the "*suppression de la reine.*" In the pteromalid *Peridesmia phytonomi*, a species in which ovarian maturation is dependent on host-feeding of the adult female, oögenesis may cease while the female is feeding daily on host fluids (Flanders, 1935). Recent studies of the parasites of black scale, *Saissetia oleae* (Bern.), show that in the case of *Metaphycus helvolus* Comp. the cessation of oögenesis occurs only when there is a lack of hosts.

Thompson and Parker (1928) observed in *Melittobia acasta* that starvation of gravid females resulted in the cessation of oögenesis and that when starved females were provided with nourishment, oögenesis was resumed. During the starvation period the eggs in the lower part of the ovaries became disorganized and were apparently absorbed. In this species the lack of sperms in the spermatheca tends to inhibit oviposition. When the spermatheca is depleted of sperms, a few unfertilized eggs may be deposited before oösorption sets in.

OVIPOSITION IN RELATION TO OVULATION

If the leading oöcyte is not absorbed, it passes into the oviduct. In most anhydropic species the egg is deposited immediately thereafter. In a few ectoparasitic forms, however, deposition may be delayed and "uterine incubation" occur. Such eggs may be deposited at random. It is noteworthy that the queen bee, deprived of cells in which to oviposit, may deposit several dozen eggs at random.

The necessity for the elimination of all eggs from the oviducts of anhydropic species is exemplified in the ichneumonid genus *Paniscus*. Embryonic development in certain species of this genus may be completed while the egg is in the oviduct. Histogenesis does not inhibit the discharge of the eggs since they pass out through a cleft at the base of the ovipositor (Vance, 1927). Several instances have been observed in which the death of the parasitic female resulted from the perforation of the wall of the oviduct by the larvae (Chewyreuv, 1912).

In hydropic species, ripe eggs may be stored in the enlarged oviducts pending conditions suitable for oviposition. Some, if not all, of the eggs may leave the ovarioles as rapidly as they are formed, independently of any external stimulus.

Pampel (1913) observed that in the "*Ophion*" type of ichneumonids such as *Campoplex*, *Angitia*, *Glypta*, *Trichomma*, etc., each of the paired oviducts is enlarged to form a "*Sammel-reservoire*" (plate I, fig. 3) for the storing of eggs. The oviducts in the "*Apanteles*" type of endoparasitic braconids (plate I, fig. 4) also are well developed for this purpose, particularly in the Microgasterinae and Cheloninae.

The paired oviducts of *Apanteles* spp., just prior to emergence of the female from its cocoon, are swollen and filled with a mass of cells (possibly mycetocytes). Oögenesis in the ovarioles is accompanied by a decrease in the numbers of these cells beginning at the base of the oviduct. The space in the oviduct vacated by the cells is concurrently filled with a

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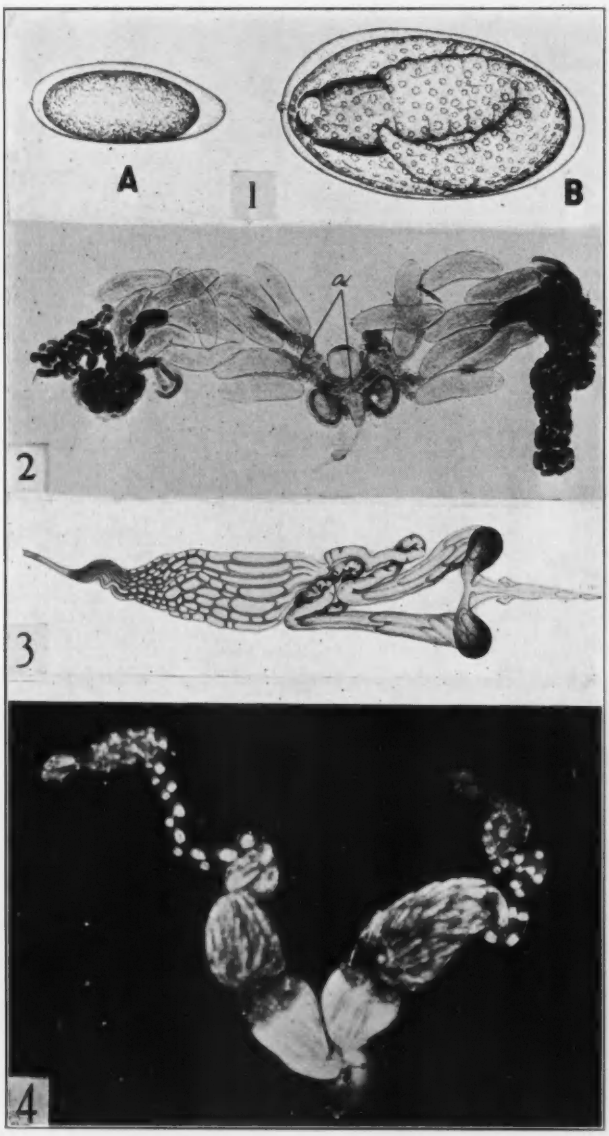
EXPLANATION OF PLATE I

Fig. 1. The hydropic egg of *Helorus paradoxus* Prov. showing trophic membrane. *A*, newly deposited egg. *B*, egg just before hatching. (After Clancy from Clausen, 1940.)

Fig. 2. The reproductive system of *Pteromalus puparum* L. with anhydropic eggs in the ovarioles. Note the short oviduct (Od).

Fig. 3. The reproductive system in the female of *Ophion luteus*. Note the enlarged oviducts for storing eggs. (After Pampel.)

Fig. 4. Ovaries of *Apanteles* sp., showing the enlarged oviducts filled with a milky fluid which apparently results from the conversion of cells (mycetocytes?) that filled the lumen of each oviduct. *S*, spermatheca.


A
1
B
a
2
3
4

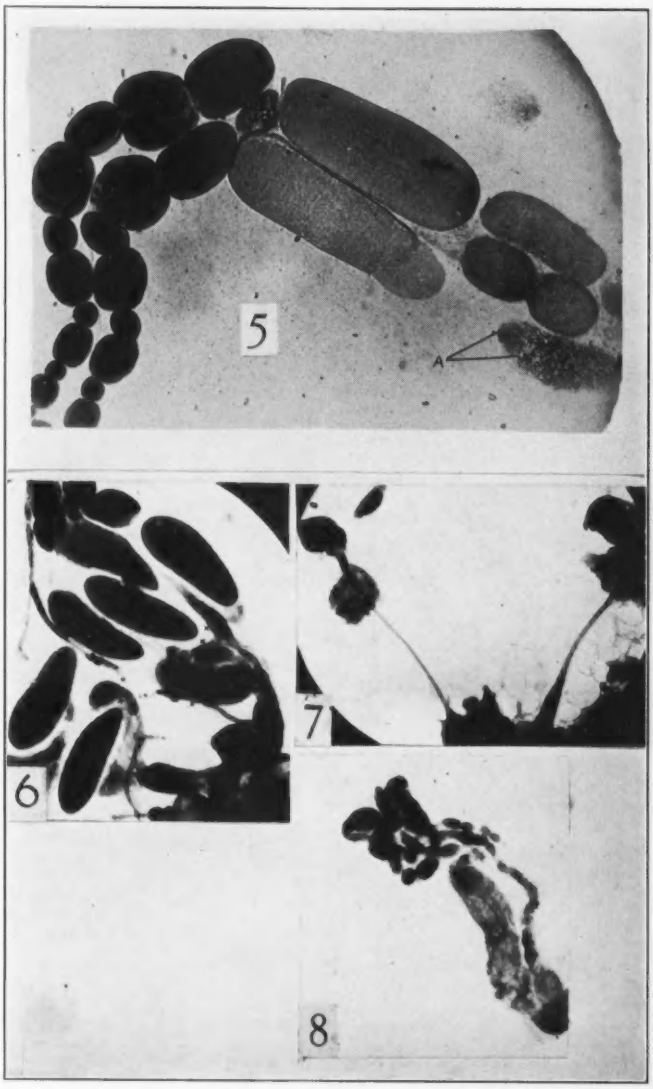
Explanation of Plate II

Fig. 5. Two ovarioles from a queen bee, showing the disintegration of the ripe eggs. *A*, the posterior yellow portion of a disintegrating egg. (The queen bees used in this study were supplied by J. E. Eckert, Associate Professor of Entomology and Associate Apiculturist in the Experiment Station, University of California.)

Fig. 6. Basal portion of the ovaries of *Dibrachoides dynastes* (Foerster) 75 days after emergence. *X*, ripe eggs in the process of sorption.

Fig. 7. Ovaries of *Peridesmia phytonomi* in state of castration, one month after emergence of female. Note that the germaria remain intact.

Fig. 8. Ovary of *Metaphycus helvolus*. Female withheld from host for 25 days and fed on a mixture of honey and host fluids. Note outline of the exochorion of the posterior body and neck of disintegrating egg. Anterior body has disappeared. The exochorion collapses and forms an egg remnant (fig. 9) in the form of a pellet.

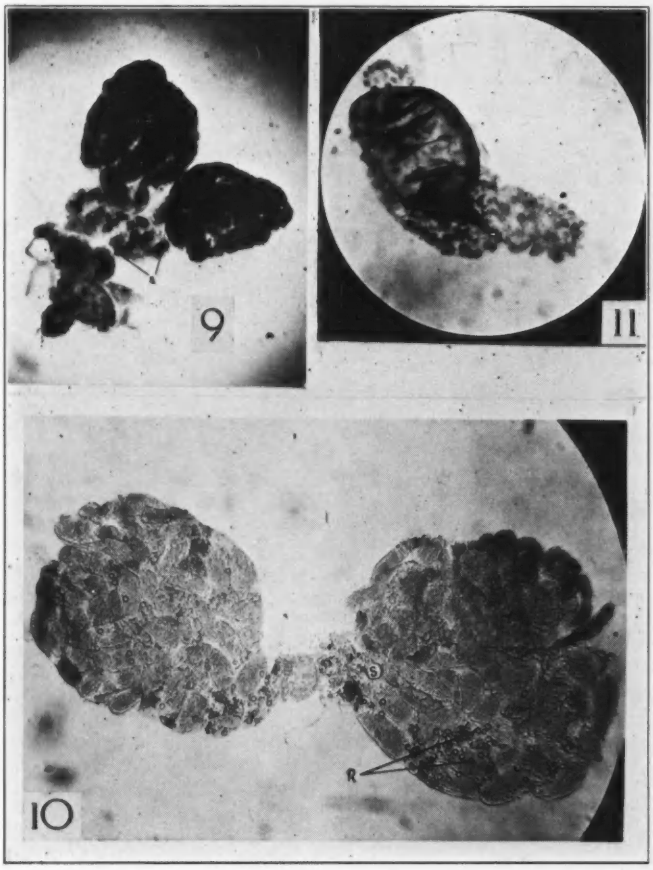

5
A
6
7
8

Explanation of Plate III

Fig. 9. Ovaries of *Metaphycus helvolus* when in a state of castration. Female withheld from host for 28 days at 80 degrees F. The number of egg remnants (e) in each pedicel indicates that 4 to 7 eggs matured and disintegrated in each of the 6 ovarioles.

Fig. 10. Ovary of *Clausenia purpurea*. *R*, "rings" which are remnants of the eggs absorbed. Each ring had encircled the neck of the double-bodied ovarian egg. The rings accumulate in the basal portion of the ovarioles. *S*, spermatheca.

Fig. 11. Exochorion of the posterior body and neck of an egg of *Encyrtus fuliginosus* after extrusion into the body cavity. The follicular cells enclosing the egg remnant gradually disappear. In this species the exochorion remains undigested.


9
11
10
S
R

milky fluid. About a week after the emergence of the female, the cells have disappeared and the milky fluid fills not only the pouch-like oviduct but the enlarged bases of the two ovarioles so that the oviduct and ovarioles together form a paired chamber or uterus, filled with eggs.

The function of this milky fluid is unknown. Under high magnification it appears to be a mass of extremely small, motile bacteria. This material may serve to retard oösorption in the bases of the ovarioles and maintain the eggs in a healthy condition pending deposition. The outer surface of the oviduct is covered with a sheathing of very fine lengthwise muscle fibers. The enlarged muscular pouch, the small eggs and the short ovipositor permit extremely rapid egg deposition.

Since development is stimulated only by substances present in the host, the eggs in the oviducts may remain in a quiescent condition during the life of the female. It is significant that in the great majority of braconid species of endoparasitic habit the egg is hydropic, increasing in size because of the absorption of host fluids by the embryo (Clausen, 1940).

The storage of ripe eggs in muscular oviducts is correlated with the ability to discharge a large number of eggs quickly during one insertion of the ovipositor or a large number singly if hosts are available. This rapidity of egg deposition probably is responsible for the fact, pointed out by Clausen (1940), that an exceptional number of braconid species yield a preponderance of male progeny.

In anhydropic species with short oviducts (plate I, fig. 2), ovulation occurs when environmental conditions are favorable for immediate egg deposition so that the rate of oviposition may be governed by the number of ovarioles (Clausen, 1940). In gregarious species, the number of eggs deposited per host may be influenced by the number of ripe eggs in the ovarioles.

In the hydropic species of *Ascogaster*, when hosts are lacking, a portion of the eggs is stored in the oviduct; then ovulation ceases and oösorption takes place in the ovarioles.

OÖSORPTION IN RELATION TO OVIPOSITION

The sorptive process in insects generally may be largely limited to the discarded egg follicles. In worker ants, however, the sorption of developing eggs has been described by Weyer (1927). He also observed that this occurred in certain wasps and in the honeybee (plate II, fig. 5). The disintegration of ripe eggs was noted by Smith (1932) in the ichneumon *Phaeogenes nigridens*. Smith's observations indicate that oösorption began in less than 10 days after the egg reached maturity.

Recently, I have observed that when certain parasitic Hymenoptera are withheld from their hosts, the processes of oösorption and oögenesis occur synchronously and enable the female, after a period of inhibited oviposition, to deposit viable eggs as if no interruption had occurred. In the prolonged absence of hosts, species in which ovulation is stimulated externally may maintain their reproductive capacity by complete oösorption and cessation of oögenesis. Such species are then in a condition of "phasic castration" (Flanders, 1935, p. 442). In other words, the function or development of gonads is temporarily inhibited.

As Lloyd (1940) has observed in the case of the ichneumonid *Diadromus collaris*, the number of eggs deposited daily may be unaffected by periods of inhibited oviposition. In several species of chalcidoids parasitic on the black scale, the substitution of oösorption for ovulation during periods of isolation apparently maintains the normal oviposition curve.

The observations substantiating this thesis have been made on several species of pteromalids parasitic on the alfalfa weevil (plate II, figs. 6 and 7) and on several encyrtids parasitic on the black scale (plate III, figs. 9 and 11). In the case of the pteromalids, oösorption may be followed by a long period of castration which begins and ends spontaneously. The encyrtids, on the other hand, lacking spontaneous castration, having very short life cycles, and being readily propagated, were better subjects for investigation.

Over 200 encyrtid females were dissected, and stained preparations were made of the ovaries. Observations on oösorption were made possible by the peculiar structure of the encyrtid egg. This egg, in the ovary, is double-bodied and, in the encyrtids under observation, possesses on the neck and posterior body a rigid band or aeroscopic plate, which seems to be superimposed on the exochorion (Maple, 1937). When the sorption of the double-bodied egg is complete, its contents and the entire anterior body have disappeared, leaving only the aeroscopic plate and all or part of the exochorion (plate III, fig. 9).

The aeroscopic plates remain more or less intact and form recognizable remnants of the ripe eggs. Such is the case when *Encyrtus fuliginosus* Comp., *Metaphycus stanleyi* Comp., *M. lounsburyi* (How.), *M. luteolus* (Timb.), *M. helvolus* Comp., *Clausenia purpurea* Ishii (plate III, fig. 10), *Habrolepis rouxi* Comp., and *Oöencyrtus johnsoni* (How.) are isolated from their host for a week or more at 80° F. A study of these species shows that oögenesis and oösorption occur synchronously and form a cyclic process which maintains a more or less constant number of ripe eggs in the ovarioles.

The egg remnants were retained in the ovarioles in most of the species examined. In *Encyrtus fuliginosus*, however, the complete exochorion of each disintegrated egg (plate III, fig. 11) appeared to have been extruded into the body cavity. In every female dissected, from 10 to 100 exochorions were found free in the body fluids. The presence of a cellular mass surrounding some of these egg shells indicates that in this case ripe eggs may be set free in the body cavity before oösorption is completed.

In this connection it is of interest to note that Thorpe and Jones (1937), in their studies of the ichneumon *Nemeritis canescens*, found dead first-stage larvae in the body cavities of gravid females. In this case, however, it seemed "fairly certain" that the eggs from which these larvae emerged were deposited by other females enclosed in the same cage, since they were frequently seen to stab one another with their ovipositors. This reaction occurred when the females were withheld from their normal hosts. Oösorption within the body fluids may have been prevented by the glandular secretion with which the eggs are coated as they pass through the oviduct (Flanders, 1934).

The ovarioles in *Encyrtus fuliginosus*, a species with non-host-feeding adults, contained a relatively large number of developing and ripe eggs, and there was little space in the base or pedicel of each ovariole for the storage of egg remnants. Consequently, the large number of exochorions found in the body cavity before and after oviposition indicates that they were extruded through the *tunica propria*, the structureless elastic membrane covering each ovariole. It is significant that ovipositing females of *E. fuliginosus* live three times as long as those that are not permitted to oviposit.

Nonviable eggs in the process of disintegration, but with the chorion intact and enclosing fluid material, may be deposited. A female of *Metaphycus luteolus*, withheld from its host for 3 weeks at 80° F., deposited both viable and nonviable, partially collapsed eggs. The ovaries of a female 4 weeks old contained developing eggs, 4 ripe eggs, and the collapsed exochorions of at least 75 ripe eggs.

Exochorions or egg remnants apparently never pass into the oviducts and consequently cannot be discharged through either the ovipositor or the copulatory opening. The accumulation of egg remnants in the pedicel, which occurs in many species, apparently does not interfere with ovulation.

The structure of the encyrtid egg precludes maturation prior to oviposition.

APPARENT RESTRAINT IN OVIPOSITION

Several investigators have shown that certain parasites distribute their eggs, not at random, but with reference to the nature of the host available at the time. Lloyd (1938) points out that the exercise of this selective faculty is dependent on the ability of the female to restrain oviposition. In his study of *Oöencyrtus kuvanae*, he found that the faculty of restraint broke down when the accumulation of ripe eggs in the ovaries reached a certain number. This occurred four days after emergence of the adult. Yet Lloyd states that "Surprisingly, when the inhibition of oviposition was extended beyond the first four days of life, restraint again became evident so that females which had been kept 10 days before being given hosts showed greater restraint than the younger females." He assumed, as have previous investigators, that the ripe eggs remained in the ovaries or oviducts until deposited. This assumption seemed verified when he found experimentally that inhibition of oviposition did "not affect the ultimate output of mature eggs provided sufficient hosts were available. . . ."

In encyrtids that are withheld from their hosts from the time of their emergence, the number of ripe eggs in the ovaries reaches a maximum within a few days. This number, however, is less than the maximum which may occur in females that have been ovipositing for several days. When such a female is withheld from its host, the ripe eggs may accumulate in the ovaries, nullifying for a short period its ability to discriminate between hosts. Subsequently, if hosts are scarce oösorption sets in and forms a cyclic process with oögenesis, so that the number of eggs that reach maturity each day is fairly constant and not excessive. As a result, the female of the anhydropic species is able to

exercise a restraint in oviposition and a choice of hosts. The faculty of oösorption therefore plays an important part in host selection and influences the efficiency of parasitization.

The females of anhydropic species may lose the ability to respond to oviposition stimuli if withheld from the host for a long time. Jackson (1937) observed that a female of the ichneumonid *Pimpla examinator*, when placed with its host after being isolated for 6 weeks, made no attempt to oviposit. Nevertheless, when dissected 2 weeks later, the presence of several "regressed eggs" indicated that oösorption was taking place.

In anhydropic species oösorption may preclude ovulation. This may account for the fact that in such species the responsiveness to oviposition stimuli appears to be a function of the frequency of oviposition.

There appears to be a distinct correlation between the degree of restraint in oviposition and the preponderance of female progeny (Flanders, 1939). This is exhibited to a marked degree in the Serphoidea (Clausen, 1940). Most of the endoparasitic species of this group probably are hydropic.

THE ROLE OF OÖSORPTION IN METAPHYCUS HELVOLUS

Since *Metaphycus helvolus* is an effective parasite of black scale, it has been studied in considerable detail. Introduced and established in California in 1937 by the University of California Citrus Experiment Station, under the direction of Professor Harry S. Smith, it now appears to be controlling the black scale throughout a large part of the state. The efficiency of this parasite may result, in part, from its ability to maintain its reproductive capacity during the prolonged absence of suitable hosts.

The normal development of the gonads in *Metaphycus helvolus*, unlike that in *Encyrtus fuliginosus* and *Metaphycus stanleyi*, is dependent on host-feeding by the adult female, since the food consumed as a larva is not sufficient for the maturation of its complement of oögonia. Oögenesis is continuous if the intervals in contacting individual hosts are not prolonged.

When the newly emerged female is isolated at a constant temperature of 80° F. and fed only on honey, oösorption begins within 3 days after emergence. Oögenesis ceases, and oösorption is complete 3 to 4 weeks after emergence. In each of the ovarioles, 4 to 7 eggs may have matured and disintegrated (plate III, fig. 9). A period of phasic castration then ensues, which ends, not spontaneously as in the pteromalids previously studied, but when contact is made with the host and the female feeds on its fluids.

When females, in a state of castration, were placed with their hosts 30 days after emerging, they began ovipositing 3 days later and deposited up to 408 eggs at the rate of from 1 to 16 per day. This production required feeding at intervals on host fluids, usually after the deposition of 1 to 5 eggs.

Phasic castration, however, does not occur if hosts are available for oviposition. The ovaries of newly emerged females of *Metaphycus*

helvolus, feeding on host fluids and honey,[6] contain no ripe eggs on the first day but may have 2 ripe eggs in each ovariole on the fourth day after emergence. Only 1 egg occurs at a time in each ovariole in females that have not fed on host fluids. A female which had been allowed to oviposit and feed on host fluids for 8 days was prevented from doing so for 24 hours and then was dissected. Each ovariole contained 3 ripe eggs. At a constant temperature of 80° F., the average number of eggs deposited daily may be as high as 12 by each female. One female produced 740 eggs, ovipositing daily over a period of 60 days. In this case, the maximum daily deposition was 18 eggs. The ovaries of females that die when hosts are available usually are entirely depleted of oöcytes and oögonia.

In *Metaphycus luteolus*, a closely related species parasitic on the same stages of black scale and having habits of development, oviposition, and feeding similar to those of *M. helvolus*, oögenesis does not cease during the life of the female. Phasic castration, therefore, apparently does not depend on either the kind or quantity of food consumed. It is significant that, regardless of the age of the castrated female, the period between contacting the host and ovipositing in it varies but little.

The feeding on host fluids that must precede oögenesis tends to increase the effectiveness of *Metaphycus helvolus* because the proportion of hosts destroyed by such feeding increases as the host density diminishes.

In this species, at a temperature of about 80° F., a primary germ cell (oögonium) becomes a ripe egg in less than 3 days. Oösorption requires considerably less time than oögenesis; probably only a few hours.

SUMMARY

In the parasitic Hymenoptera, the occurrence of oösorption prior to ovulation and the storing of ripe eggs after ovulation are adaptations for maintaining the reproductive capacity of the species when environmental conditions are unfavorable for oviposition. Eggs may be stored for periods longer than that necessary for incubation only when they are hydropic, that is, when they lack nutritive substances necessary for embryonic development.

In a certain species of *Apanteles*, the ovary and its oviduct are modified for storing its full quota of eggs.

The fact that the ripe eggs of certain species of encyrtids possess structures which are not absorbed provided proof of the synchronous nature of the oögenic-oösorptive processes that occur in many Hymenoptera.

Oösorption was found to occur only when ovulation was inhibited.

[6] According to Eckert and Allinger (1939), the average California honey consists of the following components, in percentages of the total: moisture, 16.50; total sugars, 77.53; levulose, 40.41; dextrose, 34.54; sucrose, 2.53; dextrin, 0.91; ash, 0.21; acid, 0.16; and undetermined, 4.72.

When there is a sequence of developing oöcytes in the ovarioles the leading or ripe egg is always newly formed, the preceding egg having disappeared, either through oösorption or ovulation.

Oösorption on one hand and the storing of ripe eggs on the other are adaptations permitting the restraint in oviposition which is so essential to host selection.

In the lecaniine scale parasite *Metaphycus helvolus*, the adult female of which habitually feeds on its host, the resumption of oögenesis after phasic castration is solely dependent on host-feeding.

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A SYNOPSIS OF THE GENUS SCUTIGERELLA
(Symphyla: Scutigerellidae)

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For a number of years the writer has made an effort to obtain examples of the garden centipede, *Scutigerella immaculata* (Newp.) from different parts of the world. As a result, specimens of this genus have now been received from Europe and Palestine as well as from several localities in North America. An examination of this material has shown that several species are involved and that, in a number of cases, they have been previously referred to by various authors as *S. immaculata*. One factor contributing to this situation is the fact that *S. immaculata* is a variable species. Michelbacher (1938) has previously shown that individuals molt from time to time during their entire life. Following the sixth molt they have 12 pairs of legs and the full number of scuta, but additional changes occur with the following molts, and these are particularly marked during the seventh to eleventh instars. The number of setae occuring on various parts of the body increase, anatomical proportions change, antennal segments are added, and there is an increase in body size. Thus it is no wonder then that considerable difficulty may be encountered in properly placing a species.

The fourteenth scutum of the sixth instar individual has a pair of chitinous projections arising from the posterior margin. These are lost during the next molt, but the posterior margin of the scutum has a somewhat scalloped appearance. Complete differentiation does not occur in some specimens until after the twelfth molt. Figure 1 shows some of the variations which occur in the fourteenth scutum after the different molts.

When new species are described the descriptions should be made only from individuals in which the penultimate scutum is completely or nearly completely differentiated. All of the evidence at hand indicates that the various species of *Scutigerella* have similar stages of development.

[1]It is with sincere pleasure that I express my appreciation to Professor E. O. Essig and Dr. E. Gorton Linsley for the help they have given me in the preparation of this paper.

From the material now in my possession I am here describing seven new species. Three of these are from Europe, three from the United States, and one from Palestine. This study suggests that the genus *Scutigerella* is comparatively rich in species and, as the symphylan fauna of the world become more thoroughly studied, many other species will undoubtedly be found.

There are a number of characters which are particularly useful in differentiating species. The scuta have excellent characters. Both their gross shape and the nature of the posterior margin are valuable. The scuta used in the descriptions below are the second, third, fourth, and fifteenth. It should be pointed out that the first scutum is very small, and that some workers including Hansen (1903) did not consider it

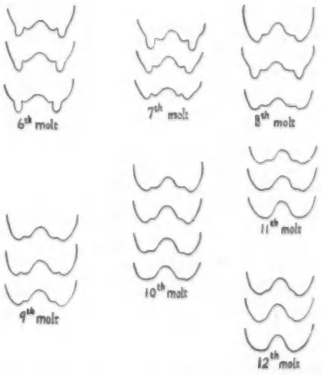

Fig. 1. Variations that occur in the penultimate scutum of *Scutigerella immaculata* in the sixth to the twelfth molts, inclusive. Note that it may be completely differentiated in the eleventh molt. (× 30). After Michelbacher (1938).

in the assignment of numbers. Therefore, in this paper the scutum referred to as number two is the first large one, or the one which Hansen regarded as scutum one. The posterior margin of scutum two ranges from nearly truncate to deeply emarginate, depending upon the species. The number of marginal and sub-marginal setae on the scuta also vary greatly in different species as does the length of the setae. It should be pointed out, however, that in a given species some intraspecific variation in the number of marginal and submarginal setae occurs. The cavity associated with the terminal segment may be of some value. In mounted specimens it is either "U"

shaped or "V" shaped, and from the material at hand it would appear that the shape is constant for any species.

The cerci also offer good characters, particularly their length as compared to their width and their length as compared to the length of the head. Their shape is of some additional value and they may be either sparsely or densely clothed with setae. Further, the length of their setae varies in different species.

There are also leg characters that can be utilized. The length of the setae as well as whether the legs are sparsely or densely clothed with setae are probably of considerable importance.

There is little doubt but what there are good antennal characters, but these are rather difficult to utilize because the antennae are broken very easily. Under such conditions they are affected by regeneration and, in addition, during molting, segments are added so that in any species a wide variation in the number of segments is likely to occur. Despite this, there appears to be some specific tendencies. The maximum number of segments likely to occur in *S. linsleyi* is probably not more than half that to be found in some of the other species.

Among the head characters, the long seta inserted between the post-antennal organ and the spiracle is very important. It may be subequal to considerably longer than the greatest width of the third antennal segment.

The body length varies greatly for the different species. *Scutigerella linsleyi* is a very small species measuring 3.5 to 4 mm. as compared to *S. silvestri* which measures 7 to 9 mm.

Although there are only eight pairs of coxal sacs in most species, in *Scutigerella verhoeffi* there are nine. This might be considered a generic character and it may later be necessary to make *S. verhoeffi* the type of a new genus. Verhoeff (1933–34) reported that he had collected specimens of what he called *S. immaculata* with both eight and nine pairs of coxal sacs, but stated he was not sure whether he was dealing with a specific difference or with an individual or local variation. Ribaut (1931) has pointed out that the last three pairs of legs in *Scolopendrella*, *Symphylella*, and *Symphylellopsis* lacked coxal sacs, while in *Symphylellina*, *Geophilella*, *Scutigerella*, and *Hanseniella* they are lacking only on the last two. In *S. verhoeffi* they are absent only on the last pair of legs.

The styli have a few characters of value. The posterior styli in some species have a secondary lateral seta.

Mounting symphylans sometimes offers considerable difficulty. Exceptionally good mounts have been obtained by the writer when the specimens were cleared in ten per cent KOH, stained for 48 hours in acetic acid fuchsin, followed by washing in acetic acid, then running through acetic acid-clove oil to straight clove oil and mounting in balsam. When considerable material has been available some specimens have been mounted in a modified Berlese's medium to which iodine has been added. These latter mounts proved exceptionally good for study.

All measurements given in this paper were made from mounted material. Some slight variation in measurements has resulted depending upon whether the material was cleared, stained, and mounted in balsam, or whole mounts were made in the modified Berlese's medium. The Berlese's medium exhibited a tendency to cause lateral expansion of some structures such as the head.

The garden centipede, *Scutigerella immaculata* (Newp.), is the best known member of the class Symphyla. This is due, in part, to the fact that it is a very serious pest of cultivated plants. The species was named by Newport (1845) from specimens collected near London, England. In some places it occurs in abundance and has been reported as doing damage to crops grown under glass by Walton (1930), Kearns and Walton (1932), Miles and Cohen (1935), and Spyer (1935). In France it has been reported as a pest by Feytaud (1925, 1926) and Larrieu (1934). Mr. Feytaud has sent me specimens from Mugron. These examples are very similar to those that occur in North America where damage by the garden centipede has been reported. Not having an opportunity to study Newport's type, I am inclined to believe that the specimens from France, the species that is destructive in England, and the one that is a pest in North America all belong to Newport's species, and I am considering them as *S. immaculata*. This species, Plate I, figures 1a to 1i is characterized by being densely clothed with relatively short setae.

Although there are a number of species of *Scutigerella*, to my knowledge *S. immaculata* is the only one that is destructive to agricultural crops. Morphologically, at least, there seems to be no reason for this restricted behavior and, as our knowledge of the genus expands, it may be found that some of the other species are capable of doing damage. At the present time an effort is being made to obtain specimens from areas throughout the

world where injury has been reported, in the hope of determining if other species are involved. The fact that *S. immaculata* attacks commercial plants may account for its wide distribution throughout much of the world. It is abundant in many nurseries and is easily transported where soil is moved from place to place.

KEY TO SPECIES OF SCUTIGERELLA

1. Posterior margin of second scutum deeply emarginate....2
   Posterior margin of second scutum subtruncate or broadly, shallowly emarginate....7
2. Femur of first pair of legs without a conspicuous ventral process....3
   Femur of first pair of legs having a very conspicuous vertical ventral process, which is from one and one-half times to more than three times longer than broad....**armata**
3. Second scutum with less than 48 marginal and sub-marginal setae....4
   Second scutum with more than 52 marginal and sub-marginal setae....6
4. Tarsus of last pair of legs sparsely set with setae; body length usually not more than 4 mm.; second scutum with not more than 38 marginal and sub-marginal setae....**linsleyi**
   Tarsus of last pair of legs moderately densely set with setae; body length usually more than 4 mm.; second scutum generally with more than 38 marginal and sub-marginal setae....5
5. Cerci with slight expansion in terminal area; sparsely set with setae, of which those at apex are slightly longer than those at the base; cavity of fifteenth scutum "U" shaped; body length 4.7 to 6.1 mm....**nodicercus**
   Cerci without slight expansion in terminal area, densely set with setae of which those at apex are not appreciably longer than those at the base; cavity of fifteenth scutum "V" shaped; body length 4.1 to 5.4 mm..**palmonii**
6. Cerci more than four times as long as greatest width, and as long as or considerably longer than length of head; posterior styli armed with a lateral seta; long seta between post-antennal organ and spiracle distinctly longer than greatest width of third antennal segment; body length 7 to 9 mm., **silvestrii**
   Cerci generally less than three and one-half times as long as their greatest width, and considerably shorter than length of head; posterior styli not armed with a lateral seta; long seta located between post-antennal organ and spiracle only about as long as the greatest width of the third antennal segment; body length less than 7 mm....**immaculata**
7. Fourth scutum without a long lateral seta on either side....8
   Fourth scutum with a long lateral seta on either side, its length equal to about the greatest width of the third antennal segment; body length 4.2 to 5.5 mm....**inculta**
8. Second scutum truncate and with from 36 to 45 marginal and sub-marginal setae; cerci about three and one-half times longer than their greatest width; cavity of fifteenth segment "U" shaped; eight pairs of fully developed coxal sacs; body length 4.3 to 5.2 mm....**causeyae**
   Second scutum barely emarginate and with more than 45 marginal and sub-marginal setae; cerci about four times longer than their greatest width; cavity of fifteenth segment "V" shaped; nine pairs of fully developed coxal sacs; body length 4.9 to 7.8 mm....**verhoeffi**

Scutigerella biscutata Bagnall (Bagnall, 1914) has proven to be a sixth instar individual of *S. immaculata*. This was verified by specimens sent to Mr. Bagnall for comparison with his types.

The species *Scutigerella spinipes* Bagnall (Bagnall, 1914) is insufficiently described to be recognizable. I am inclined to believe that it is approximately a seventh instar individual of *S. immaculata* but I was unable to substantiate this through specimens sent to Mr. Bagnall.

Scutigerella silvestrii n. sp.

(Plate I, figs. 2a to 2i)

Head slightly wider than long, central rod (coronal suture) complete in its entire length, although less distinct in its anterior portion; lateral branches arise near base of head and continue diagonally to a point just posterior and to the outside of the post-antennal organs; anterior branches (frontal sutures) present. Long seta located between post-antennal organ and spiracle distinctly longer than greatest width of the third antennal segment. Top of head set with setae of several lengths; between the lateral branches and the side of the head there are a number of very long setae; longest are about four times the length of the shortest setae found in the same general area.

Right *antenna* of the type broken, left of 33 segments. Antennae broken in most of the specimens examined. Largest number found in any specimen was 44, although more than this number can be expected to occur in the species. Second antennal segment with three setae on dorsal surface of which the outer one is much thicker and more developed than the others. Outer setae on other basal segments more strongly developed than those on inner side. On dorsal surface of third antennal segment just anterior to the primary row of setae and in medial position there is a strong short spine. In the type a similar spine is found on the fourth and fifth segment. Second whorl of setae starts on the tenth or eleventh segment. Apical segment with a large stalked organ set on a prominent base; a small sensory organ is also present. Organs similar to the latter may be found on dorsal surface and to the outside on all segments beginning with the fifth, sixth, or seventh to apical one. In prepared mounts the membranous anterior portion of the next to the last segment somewhat expanded.

The second *scutum* with about 55 marginal and sub-marginal setae, and with posterior margin rather strongly emarginate; third scutum with about 64 marginal and sub-marginal setae and with posterior margin rather deeply emarginate, fourth scutum with about 60 marginal and sub-marginal setae, and with its posterior margin emarginate. All three scuta with several long setae along the lateral edges. They are sub-marginal as compared to the shorter setae. The longest of these setae on second scutum about three times the length of the shortest

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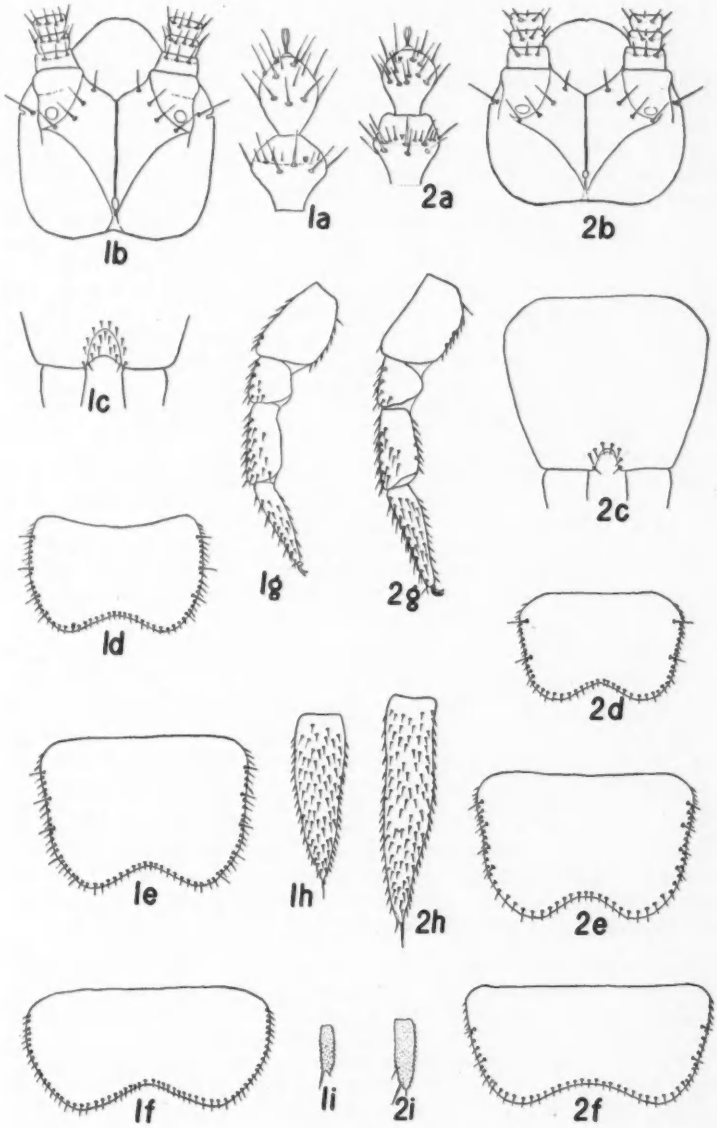
EXPLANATION OF PLATE I

Fig. 1. *Scutigerella immaculata* (Newp.). 1a, dorsal view of last two segments of antenna; 1b, head and first four antennal segments, only the long setae on anterior half of head and those on the antennal segments are shown; 1c, cavity associated with fifteenth scutum, only the setae in or close to the cavity are drawn in; 1d to 1f, second, third, and fourth scuta, only marginal setae and the longer sub-marginal setae are shown; 1g, posterior view of twelfth leg; 1h, cercus; 1i, stylus. (All × 68 except 1a, which is × 180, and 1i, which is × 90.)

Fig. 2. *Scutigerella silvestri* n. sp. 2a, dorsal view of last two segments of antenna; 2b, head and first four antennal segments, only the long setae on anterior half of head and those of the antennal segments are shown; 2c, cavity associated with fifteenth scutum, only the setae near or close to the cavity are shown; 2d to 2f, second, third, and fourth scuta, only marginal setae and the longer sub-marginal setae are shown; 2g, posterior view of twelfth leg; 2h, cercus; 2i, stylus. (All × 45 except 2a and 2i × 90.)


1b
1a
2a
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1c
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2c
1d
2d
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1i
2i
2f

lateral setae. In case of the third scutum the longest lateral setae only about two and one-half times the length of the shortest marginal setae, and in case of the fourth scutum only about twice as long. Setae of fifteenth scutum not carried into the cavity. *Trochanter* of last pair of legs without setae on posterior surface, one or two on outer surface, several on inner surface and entire anterior surface sparsely covered; *femur* with several setae on posterior surface, seven or eight on outer surface, some on inner surface, and seven or eight sparsely scattered setae on anterior surface. *Tibia* with about eight setae on posterior surface about 14 arranged in two rows on outer surface, a number on inner surface, and anterior surface well covered with setae; *Tarsus* with posterior surface well covered, outer surface with about 18 setae arranged in two rows, a row of setae on inner surface and a rather large number on the anterior surface, the most of which are very short; tarsus at least three and one-half times as long as wide; anterior *claw* somewhat more robust than posterior one, but not so strongly curved. Inner surface of trochanter of second pair of legs armed with two long setae the longest of which is more than one-half the width of the segment. *Styli* well developed; about three times as long as their grestest width, covered with numerous short hairs; armed at apical end with one short and one well developed seta; below the large seta and about two-thirds from base of stylus there is another well developed although smaller seta. *Calicles* from which posterior sensory setae (trichobothria) arise surrounded by branched setae; on inner margin of ring of branched setae there are two strong spines. *Cerci* about four and two-tenths times as long as their greatest width; rather densely covered with moderately short setae; terminal area small and facing outward. *Length* seven to nine mm.

Holotype No. 5190. Calif. Acad. Sci. Ent., Portici, Italy. Described from nine specimens sent to me by Dr. F. R. Silvestri, under a letter dated December 20, 1933. The species can be separated from other members of the genus except *S. verhoeffi* by the long slender cerci. It may be distinguished from *S. verhoeffi* by the fact that the posterior margin of the second, third, and fourth scuta are deeply emarginate, whereas in *S. verhoeffi* the posterior margins of the three mentioned scuta are only slightly emarginate. *S. silvestri* is the largest species that I have yet encountered. Among the specimens at hand there is a seventh instar individual which is seven and one-half mm. in length. Only one antenna was unbroken and this contained 37 segments, a large number when compared to a similar stage of *S. immaculata* which normally has 24 to 27 antennal segments.

Scutigerella palmonii n. sp.
(Plate II, figs. 1a to 1i)

Head slightly longer than wide, central rod (coronal suture) complete in its entire length, although less distinct in its anterior portion; lateral branches arise near base of head and continue diagonally to a point just

posterior and to the outside of the post-antennal organs; anterior branches (frontal sutures) present. Long seta located between post-antennal organ and spiracle only about as long as the greatest width of third antennal segment. Top of head set with setae of several lengths; between lateral branches and side of head there are a number of long setae, the longest about three times the length of the shortest found in the same general area.

Antennae broken on most specimens; where complete the number of segments ranged from 32 to 36. Second antennal segment with three setae on dorsal surface, of which the outer one is thicker and more strongly developed. Outer setae on other basal segments larger than those on inner surface; on dorsal surface of third antennal segment just anterior to primary row of setae and in medial position there is a strong short spine; second whorl of setae starts on sixth to ninth segment. Apical segment with large stalked organ set on prominent base; one or two smaller sensory organs also present; organs similar to the latter may be found on dorsal surface and to the outside on all segments from sixth or seventh to apical segment.

Second *scutum* with from 36 to 44 marginal and sub-marginal setae of several lengths and with posterior margin moderately emarginate, third scutum with from 45 to 57 marginal and sub-marginal setae of several lengths and with posterior margin emarginate; fourth scutum with from 45 to 55 marginal and sub-marginal setae of several lengths and with posterior margin emarginate. On all three scuta the longest lateral setae tend to be sub-marginal as compared to the shorter setae. Longest lateral setae on fourth scutum hardly one-half the greatest width of third antennal segment. Cavity of fifteenth scutum "V" shaped and setae not carried into it. *Trochanter* of last pair of legs without setae on posterior surface, anterior surface set with rather short setae, outer surface with two or three setae near distal end, and inner surface with a row of setae.

Femur with one seta on outer distal margin of posterior surface, anterior surface set with about five or six rather small setae, outer surface with several large setae and inner surface devoid of setae. Posterior surface of *tibia* set with several setae on outer half, anterior surface sparsely set with rather small setae, outer surface clothed with well-developed setae, one row of which stands rather erect, the inner surface set with a row of rather small setae. Posterior surface of *tarsus* set with setae on outer two-thirds, anterior surface sparsely set with small setae, outer surface with a row of setae that stand rather erect, and inner surface with a row of rather short setae. Tarsus a little more than three and one-half times as long as its greatest width. Anterior *claw* somewhat more robust than posterior one but not so strongly curved. *Styli* well developed not quite four times as long as wide, covered with numerous short hairs, armed at apical end with one short and one well developed seta, no other seta present. *Calicles* from which long posterior sensory setae (trichobothria) arise surrounded with branched setae. *Cerci* about three and six-tenths times as long as their greatest width, well covered with setae, and with terminal area small and facing outward. *Coxal sacs* located at bases of third to tenth pair of legs inclusive. *Length* 4.1 to 5.4 mm.

Holotype No. 5191. Calif. Acad. Sci. Ent., Palestine. Described from eleven adult specimens sent me by Mr. J. Palmoni under a letter dated May 27, 1940. The specimens were collected on the eastern bank of the River Jordan, near its emergence from the Lake of Galilee, at an elevation of about 200 meters below sea level. This species is most closely related to *S. nodicercus*, but the cerci lack the slight expansion of the terminal area, and are more densely clothed with setae. Further, the cavity of the fifteenth scutum is "V" shaped, while in *S. nodicercus* it is "U" shaped.

Scutigerella nodicercus n. sp.

(Plate II, figs. 2a to 2i)

Head slightly longer than wide, central rod (coronal suture) complete in its entire length, although less distinct in its anterior portion; lateral branches arise near base of head and continue diagonally to a point just posterior and to the outside of the post-antennal organs; anterior branches (frontal sutures) present. Long seta located between post-antennal organ and spiracle about as long as the greatest width of the third antennal segment. The two long setae located nearest post-antennal organ on sclerite defined by the lateral and frontal sutures, posterior to post-antennal organ and nearly in line with the horizontal axis of the head. Top of head set with setae of several lengths, between lateral branches and side of head there are a number of long setae; the longest about three times the length of the shortest found in same general area. Number of *antennal* segments ranging from 27 to 38.

Second antennal segment with three setae on dorsal surface, of which the outer one is thicker and more strongly developed. Outer setae on other basal segments larger than those on inner surface; on dorsal surface of third antennal segment just anterior to primary row of setae and in medial position there is a strong short spine; second whorl of setae starts on sixth or seventh segment. Apical segment with large stalked organ set on prominent base; a smaller sensory organ also present, organs similar to latter may be found on dorsal surface and to the out-

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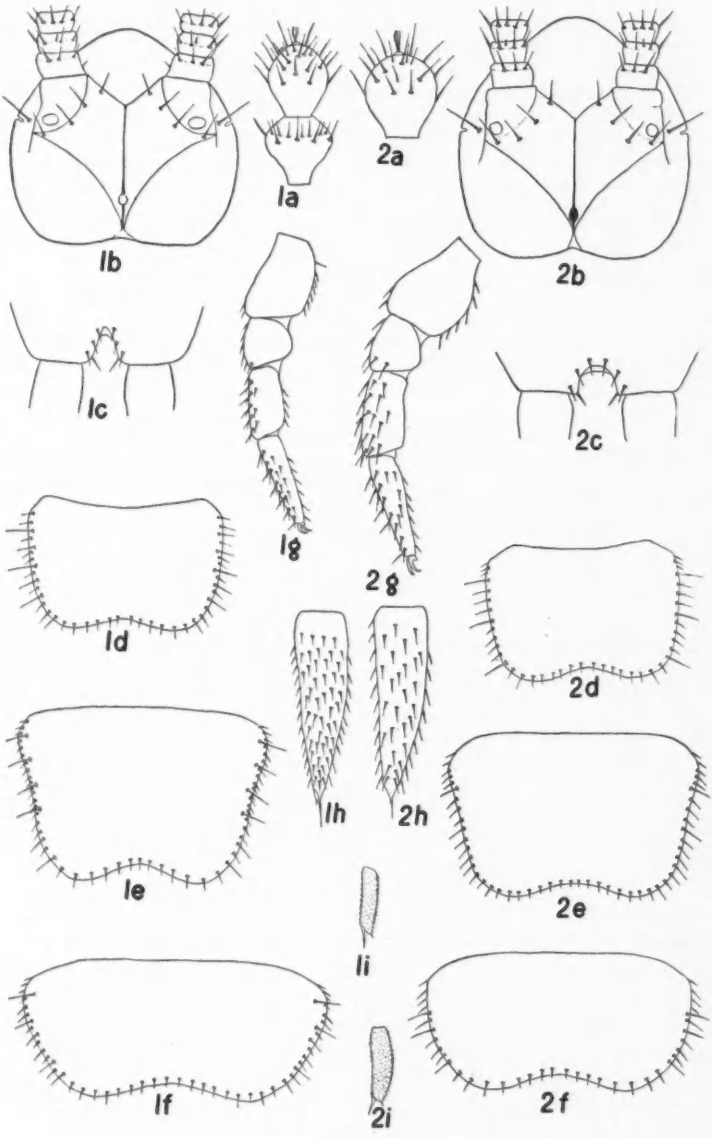
EXPLANATION OF PLATE II

Fig. 1. *Scutigerella palmonii* n. sp. 1a, dorsal view of last two segments of antenna; 1b, head and first four antennal segments, only the long setae on anterior half of head and those of the antennal segments are shown; 1c, cavity associated with fifteenth scutum, only the setae in or close to the cavity are drawn; 1d to 1f, second, third and fourth scuta, only marginal setae and the longer sub-marginal setae are shown; 1g, posterior view of twelfth leg; 1h, cercus; 1i, stylus. (All × 80 except 1a and 1i, × 160.)

Fig. 2. *Scutigerella nodicercus* n. sp. 2a, dorsal view of last antennal segment; 2b, head and first four antennal segments, only the long setae on anterior half of head and those of the antennal segments are shown; 2c, cavity associated with fifteenth scutum, only setae in or close to the cavity are drawn; 2d to 2f, second, third, and fourth scuta, only marginal setae and the longer sub-marginal setae are shown; 2g, posterior view of twelfth leg; 2h, cercus; 2i, stylus. (All × 80 except 2a and 2i, × 160.)


1a
2a
1b
2b
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1d
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2i
2f

side on all segments from the seventh or eighth to apical segment. Second scutum with from 32 to 44 marginal and sub-marginal setae of several lengths and with posterior margin only moderately emarginate; third scutum with 36 to 48 marginal and sub-marginal setae of several lengths and with the posterior margin moderately emarginate; fourth scutum with 38 to 40 marginal and sub-marginal setae of several lengths and with posterior margin moderately emarginate. On all three scuta the longest lateral setae tend to be sub-marginal as compared to the shorter setae. Longest lateral setae on fourth scutum only a little more than one-half the greatest width of the third antennal segment. Cavity of fifteenth scutum "U" shaped and setae not carried into it.

Trochanter of last pair of legs without setae on posterior surface, anterior surface set with rather short setae, outer surface with two or three setae near distal end, and inner surface with a row of setae. *Femur* with about two setae on outer distal margin of posterior surface, anterior surface set with about five rather small setae, outer surface with several large setae and inner surface devoid of setae. Posterior surface of tibia set with numerous setae on outer half, anterior surface sparsely set with small setae, outer surface clothed with well developed setae, and none found on inner surface. Posterior surface of *tarsus* set with setae, anterior surface covered with short setae; outer surface with a row of setae that stand rather erect, and inner surface with a row of short setae. Tarsus about three and one-half times as long as its greatest width. Anterior claw somewhat more robust than posterior one but not so strongly curved. *Styli* well developed about three and one-half times as long as their greatest width covered with numerous short hairs, armed at apical end with one short and one well developed seta, no other seta present. *Calicles* from which the long posterior sensory setae (trichobothria) arise surrounded with branched setae. *Cerci* about three and six-tenths times as long as their greatest width, well covered with moderately large setae; those at apical end slightly longer than those at base, terminal area small and faces outward, slightly expanded. *Coxal sacs* located at bases of third to tenth pair of legs inclusive. *Length* 4.7 to 6.1 mm.

Holotype No. 5192. Calif. Acad. Sci. Ent., Salsburg, Germany. Described from seven specimens sent by Dr. K. W. Verhoeff from Salsburg and Oberbayern, Germany, with a letter dated April 14, 1938. The specimens from Oberbayern were collected at an elevation of 1000 to 1450 meters. This species is most closely related to *S. palmonii* and the characters which separate them are considered under the latter species. It is also closely related to *S. inculta* but on the fourth scutum there is no long lateral seta such as is found in the latter. The slight expansion of the terminal area of the cerci is also a difference worthy of note. The cavity of the fifteenth scutum is "U" shaped whereas in *S. inculta* it is more "V" shaped. Finally, there is no lateral seta on the styli such as found in *S. inculta*.

Scutigerella verhoeffi n. sp.

(Plate III, figs. 1a to 1i)

Head about as wide as long, central rod (coronal suture) complete in its entire length, although slightly less distinct in its anterior portion; lateral branches arise near base of head and continue diagonally to a point just posterior and to the side of the post-antennal organs; anterior branches (frontal sutures) present. Long seta located between post-antennal organ and spiracle considerably longer than the width of the third antennal segment. Top of head set with setae of several lengths; between lateral branches and side of head there are a number of long setae, the longest about four times the length of shortest setae found in the same area. Number of *antennal* segments ranged from 39 to 53. Second antennal segment with three setae on dorsal surface of which the outer one is thicker and more developed; outer setae on other basal segments larger than those on inner surface; on dorsal surface of third antennal segment just anterior to primary row of setae and in medial position there is a strong short spine; second whorl of setae starts on eighth to thirteenth segment; apical segment with large stalked organ set on prominent base; one or two small sensory organs also present; organs similar to latter may be found on dorsal surface and to the outside on all segments from seventh or eighth to apical segment.

The second *scutum* with from 47 to 55 marginal and sub-marginal setae of several lengths and with the posterior margin only slightly emarginate; third scutum with from 58 to 73 marginal and sub-marginal setae of several lengths and with the posterior margin slightly emarginate; fourth scutum with 56 to 72 marginal and sub-marginal setae of several lengths and with hind margin slightly emarginate. On all three scuta the longest lateral setae are sub-marginal as compared to shorter setae. Cavity of fifteenth scutum "V" shaped and in only one out of four specimens were setae carried into it. *Trochanter* of last pair of legs without any setae on posterior surface, anterior surface set with setae, outer surface with two or three setae near the posterior end, and inner surface with a row of setae. *Femur* with three or four setae on outer distal margin of posterior surface, anterior surface set with seven or eight setae, outer surface with setae, and none on inner surface. Posterior surface of *tibia* set with setae on outer half, entire anterior surface set with setae, as is outer surface, and none on inner surface. Posterior surface of *tarsus* with setae on outer two-thirds, anterior surface set with rather short setae, outer surface set with large setae, and inner surface set with setae that are shorter than those on outer surface. Tarsus about four times as long as its greatest width. Anterior *claw* somewhat more robust than posterior one but not so strongly curved. *Styli* well developed about four times as long as their greatest width, covered with numerous short hairs, armed at apical end with one short and one well developed seta, no other setae present. *Calicles* from which the long posterior sensory setae (trichobothria) arise surrounded with branched setae. *Cerci* about four times as long as their greatest width, well covered with moderately short setae, terminal area small and facing outward. *Coxal sacs* located at bases of third to eleventh pair of legs inclusive. Thus there are nine pairs instead of the usual eight pairs. *Length* 4.9 to 7.8 mm.

Holotype No. 5196. Calif. Acad. Sci. Ent., probably from the Austrian Alps in southern Germany. Four specimens were sent me by K. W. Verhoeff with a letter dated April 14, 1938. The label on the vial is poorly written, but examples are presumably from the locality above mentioned. This species is most closely related to *S. causeyae* but it is larger, more marginal and sub-marginal setae are found on the scuta, and the cerci are about four times as long as their greatest width (in *S. causeyae* they are only about three and four-tenths times as long as wide). In addition, the cavity of the fifteenth scutum is "V" shaped while in *S. causeyae* it is more "U" shaped. Finally, there are nine pairs of coxal sacs which is a very distinctive feature.

Scutigerella causeyae n. sp.

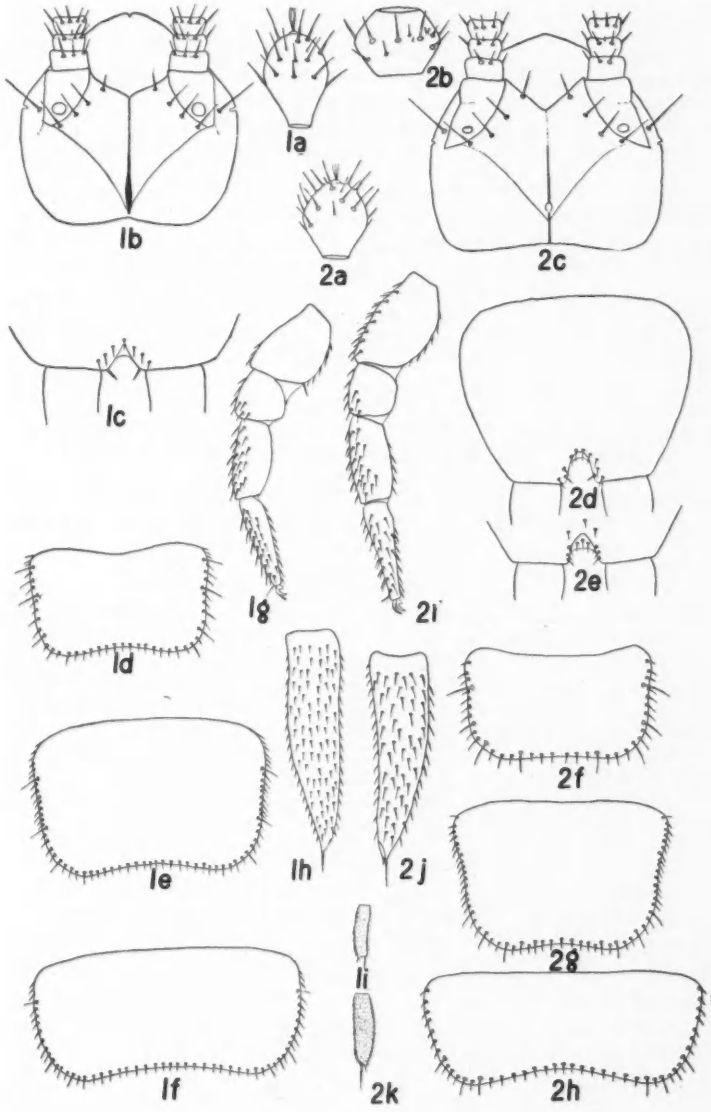
(Plate III, figs. 2a to 2k)

Head about as wide as long, central rod (coronal suture) complete in its entire length, although less distinct in its anterior portion, lateral branches arise near base of head and continue diagonally to a point just posterior and to the outside of the post-antennal organs; anterior branches (frontal sutures) present; long seta located between post-antennal organ and spiracle at least one and three-tenths times longer than the width of the third antennal segment. Top of head set with setae of several lengths; between the lateral branches and side of head there are several long setae; longest are only about two times the length of the shortest setae found in same general area. *Antennae* in most specimens broken or appeared to have been regenerated, number of segments in individuals with normal appearing antennae ranged from 29 to 38. Second antennal segment with three setae on dorsal surface of which the outer one is the largest; outer setae on other basal segments considerably thicker than those on inner side. On dorsal surface of third antennal segment just anterior to primary row of setae and in medial position there is a strong short spine; second whorl of setae starts at about the seventh segment. Apical segment with large stalked organ set on prominent base; one or two smaller sensory organs also present.

EXPLANATION OF PLATE III

Fig. 1. *Scutigerella verhoeffi* n. sp. 1a, dorsal view of last antennal segment; 1b, head and first four antennal segments, only the long setae on anterior half of head and those of the antennal segments are shown; 1c, cavity associated with fifteenth scutum, only the setae in or close to the cavity are shown; 1d to 1f, second, third, and fourth scuta, only marginal and the longer sub-marginal setae are shown; 1g, posterior view of twelfth leg; 1h, cercus; 1i, stylus. (All × 64 except 1a, × 128 and 1i × 85.)

Fig. 2. *Scutigerella causeyae* n. sp. 2a, dorsal view of last antennal segment; 2b, dorsal view of twelfth antennal segment; 2c, head and first four antennal segments, only the long setae on anterior half of head and those of the antennal segments are shown; 2d and 2e, cavity associated with fifteenth scutum, only the setae in or close to the cavity are shown; 2f to 2h, second, third, and fourth scuta, only marginal and the longer sub-marginal setae are shown; 2i, posterior view of twelfth leg; 2j, cercus; 2k, stylus. (All × 85 except 2a, 2b, and 2k, × 170.)


1b
1a
2b
2a
2c
1c
1g
2i
2d
2e
1d
1h
2j
2f
1e
2g
1i
1f
2k
2h

Organs similar to the latter found on dorsal surface and to the outside on all segments from the fifth, sixth, or seventh to apical segment.

Second *scutum* with from 38 to 44 marginal and sub-marginal setae of several lengths and with the posterior margin truncate or barely emarginate; third scutum with from 54 to 57 marginal and sub-marginal setae of several lengths and with posterior margin only slightly emarginate; fourth scutum with 48 to 50 marginal and sub-marginal setae of several lengths and with the posterior margin distinctly emarginate. On all three scuta the longest setae tend to be sub-marginal as compared to the shorter setae; longest setae of second scutum slightly more than twice the length of the shortest; in case of third and fourth scuta the longest setae only about twice the length of the shortest; both third and fourth scuta devoid of any very long setae. Setae of fifteenth scutum rarely carried into cavity. *Trochanter* of last pair of legs without any setae on posterior surface, anterior surface sparsely set with setae, outer surface well armed with setae, and at least a row of setae on inner surface. *Femur* with two or three setae on posterior surface, three or four on anterior surface, well clothed on outer surface and none on inner surface. *Tibia* well clothed with setae on outer half of posterior surface, sparsely set with relatively short setae on anterior surface, well clothed on outer surface, and with a row of four or five setae on inner surface; *tarsus* well armed with setae on posterior surface, anterior surface sparsely clothed with relatively short setae, outer surface with a row of eight or nine setae and inner surface with a row of setae; tarsus about four times as long as its greatest width.

Anterior *claw* somewhat more robust than posterior one but not so strongly curved. Inner surface of trochanter of second pair of legs armed with several large setae whose length is considerably more than one-half the width of the segment, *Styli* well developed, about three and one-half times as long as their greatest width, covered with numerous short hairs; armed at apical end with one short and one well developed seta, no other seta present. *Coxal sacs* located at bases of third to tenth pair of legs inclusive. *Calicles* from which the posterior sensory setae (trichobothria) arise surrounded with branched setae. *Cerci* about three and four-tenths times as long as their greatest width; rather densely clothed with moderately short setae; terminal area small and facing outward. Length 4.3 to 5.2 mm.

Holotype No. 5193. Calif. Acad. Sci. Ent., Durham, North Carolina, May, 1940. Described from eighteen specimens sent me by Dr. N. B. Causey. With the exception of *S. verhoeffi* this species is easily distinguished from other members of the genus by the shape of the scuta, and by the very slight emargination of their posterior margins. The number of marginal and sub-marginal setae on the second, third, and fourth scuta are less than found in *S. silvestri* and *S. immaculata* but more than found in *S. inculta* and *S. linsleyi*. The length of the setae on these scuta is relatively shorter than those found in the latter two species. Characters that distinguish it from *S. verhoeffi* are

considered under the latter species. It might be added that the posterior margin of the second scutum is truncate, whereas in *S. verhoeffi* it is barely emarginate.

Although the largest number of antennal segments represented in the series is 38, the highest possible number probably considerably exceeds this. This opinion is based on the fact that in the material in my possession there are a sixth and a seventh instar individual each with its antennae complete. The sixth instar specimen has 24 and 25 segments in the antennae while the seventh instar individual has 27 segments. For the same stage individuals in *S. immaculata* the range for the respective stages is 20 to 24 and 24 to 27 (Michelbacher, 1938). Old specimens of *S. immaculata* may finally develop as many as 60 segments in the antennae. Because of the similar number of segments found in the younger instars of the two species it is reasonable to believe that old individuals of *S. causeyae* would probably develop approximately as many segments as found in *S. immaculata*.

Apparently *S. causeyae* is a species that occurs in uncultivated areas. All the specimens sent me were collected in forested regions.

Scutigerella linsleyi n. sp.

(Plate IV, figs. 1a to 1i)

Head slightly longer than wide, central rod (coronal suture) complete in its entire length; lateral branches arise near base of head and continue diagonally to a point just posterior and to the outside of the post-antennal organs; anterior branches (frontal sutures) present. Long setae located between post-antennal organ and spiracle slightly shorter than width of third antennal segment. Left *antenna* of type broken, right of 23 segments. Dorsal surface of second segment with three setae of which the outer one is much the larger; second whorl of setae begins at about the seventh segment. Apical segment with large stalked organ, and either one or two other very small sensory organs. Other sensory organs similar to the latter are found in the type on all segments from the seventh on with the exception of the eighteenth which has none. Their location is dorsal and to the outside of the segment and almost in line with row of primary setae. In the species there is some variation in the number of segments that carry these sensory organs.

The second *scutum* with from 33 to 36 marginal and sub-marginal setae of several lengths; the longest are found along the lateral edges, and are about twice the length of shortest setae; hind margin of scutum deeply emarginate. Third scutum with from about 40 to 44 marginal and sub-marginal setae of several lengths and with the hind margin deeply emarginate. Fourth scutum with from 37 to 42 marginal and sub-marginal setae of several lengths, the longest of these about twice

the length of the shortest, hind margin of scutum strongly emarginate. Setae of fifteenth scutum not carried into cavity. ***Trochanter*** of last pair of legs without setae on posterior surface, anterior surface sparsely set with setae, outer surface with setae at distal end and inner surface with a row of several setae; ***Femur*** with one or two setae on outer edge of posterior surface, three or four setae on anterior surface, about four arranged in two rows on outer surface and none on inner surface; *Tibia* with about six setae on the outer posterior surface, anterior surface very sparsely set with smaller setae, a row of four on outer surface and none on inner surface; *Tarsus* with about seven setae on posterior surface, anterior surface sparsely set with very small setae, a row of three or four setae on the outer surface, and about two setae on inner surface; *Tarsus* about three and one-half times as long as its greatest width. Anterior *claw* slightly more robust than the posterior one but not quite so strongly curved. The inner side of trochanter of the second pair of legs armed with several large setae, the largest of which is one-half the greatest width of the segment. *Styli* well developed, about three times as long as wide, covered with numerous short hairs armed at apical end with one short and one long well developed seta. *Coxal sacs* located at bases of third to tenth pair of legs inclusive. *Calicles* from which the posterior sensory setae (trichobothria) arise surrounded by branched setae. *Cerci* about three and two-tenths times as long as their greatest width; covered with rather long sparsely set setae; terminal area small and facing outward. *Length* three and one-half to four mm.

Holotype No. 5194. Calif. Acad. Sci. Ent., Idyllwild, California, April 11, 1939. Described from seven specimens collected in a loamy soil on a slope covered with rather dense growing brush. The species was taken at an elevation of about a mile and thus far no specimens have been found in any other locality. *S. linsleyi* can be separated from other members of the genus by its small size and fewer setae on the tarsus and cerci. The scuta are very deeply emarginate, their shape is different than that of other species, and they bear relatively fewer marginal and sub-marginal setae. A very distinctive character is the

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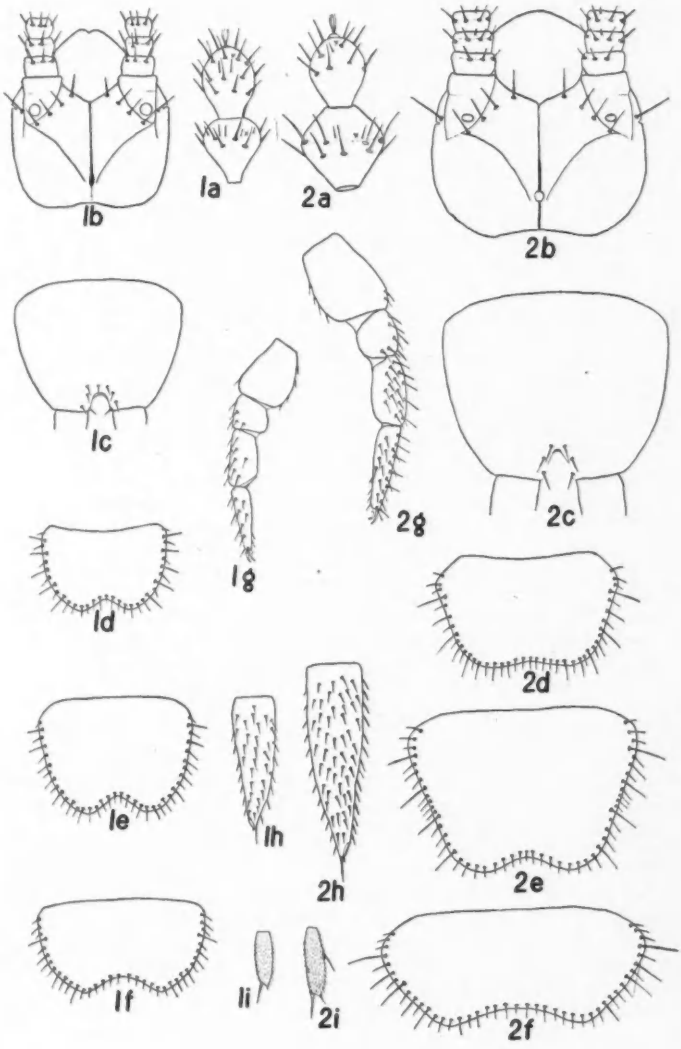
EXPLANATION OF PLATE IV

Fig. 1. *Scutigerella linsleyi* n. sp. 1a, dorsal view of last two antennal segments; 1b, head and first four antennal segments, only the long setae on anterior half of head and those of the antennal segments are shown; 1c, cavity associated with fifteenth scutum, only setae in or close to the cavity are shown; 1d to 1f, second, third, and fourth scuta, only marginal and the longer sub-marginal setae are shown; 1g, posterior view of twelfth leg; 1h, cercus; 1i, stylus. (All × 85 except 1a and 1i, × 170.)

Fig. 2. *Scutigerella inculta* n. sp. 2a, dorsal view of last two antennal segments; 2b, head and first four antennal segments, only the long setae on the anterior half of head and those of the antennal segments are shown; 2c, cavity associated with the fifteenth scutum, only setae in or close to the cavity are shown; 2d to 2f, second, third, and fourth scuta, only marginal and the longer sub-marginal setae are shown; 2g, posterior view twelfth leg; 2h, cercus; 2i, stylus. (All × 85 except 2a and 2i, × 170.)


1b
1a
2a
2b
1c
2g
2c
1g
1d
2d
1e
1h
2h
2e
1f
1i
2i
2f

relatively few antennal segments. None of the specimens had more than 23 segments even though the fourteenth scutum was completely differentiated.

Scutigerella inculta n. sp.
(Plate IV, figs. 2a to 2i)

Head nearly as wide as long, central rod (coronal suture) complete in its entire length, although less distinct in its anterior portion; lateral branches arise near base of head and continue diagonally to a point just posterior and to the outside of the post-antennal organs; anterior branches (frontal sutures) present. Long seta located between post-antennal organ and spiracle at least as long or considerably longer than the greatest width of the third antennal segment. Top of head set with setae of several lengths; between lateral branches and side of head there are a number of long setae, the longest about three times the length of shortest setae found in same general area. Number of *antennal segments* in large specimens ranged from 27 to 34. Second antennal segment with three setae on dorsal surface of which the outer one is the most developed. Outer setae on other basal segments just slightly more developed than those on inner side. On dorsal surface of third antennal segment just anterior to primary row of setae and in medial position there is a strong short spine; second whorl of setae starts on seventh or eighth segment. Apical segment with large stalked organ set on prominent base; a smaller sensory organ also present. Organs similar to the latter may be found on dorsal surface and to the outside on all segments from sixth or seventh to apical segment.

Second *scutum* with 33 to 42 marginal and sub-marginal setae of several lengths, and with posterior margin only slightly emarginate; third scutum with 41 to 47 marginal and sub-marginal setae of several lengths, and with posterior margin rather deeply emarginate; fourth scutum with 39 to 43 marginal and sub-marginal setae of several lengths and with posterior margin distinctly emarginate. There is a very long lateral seta which is considerably longer than width of third antennal segment. On all three scuta the longest lateral setae tend to be slightly sub-marginal as compared to the shorter setae; longest of these setae on second scutum about three times the length of shortest setae; in third scutum longest lateral setae at least three times length of shortest marginal setae; and in fourth scutum about three times as long. Long lateral setae are also found on scuta five to ten inclusive. Setae of fifteenth scutum not carried into cavity. *Trochanter* of last pair of legs without setae on posterior surface, anterior surface sparsely set with setae, outer surface with two or three setae near posterior end, and inner surface with a row of setae; *Femur* with one or two setae on posterior surface, about five on anterior surface, outer surface with five or six setae arranged in two rows and none on inner surface; *Tibia* with about ten setae on posterior surface, about six sparsely set setae on the distal two-thirds of anterior surface, three rows of setae on outer surface of which setae of center row are larger and more erect, and no setae on inner surface; posterior surface of *tarsus* sparsely set with setae, anterior surface on distal two-thirds sparsely set with smaller setae, outer

surface with a row of erect setae; these are slightly more erect than the row found on outer surface of tibia; inner surface with a row of setae on distal half. Tarsus nearly four times as long as its greatest width.

Anterior *claw* somewhat more robust than posterior one but not so strongly curved. Inner surface of trochanter of second pair of legs armed with several large setae, whose length is about one-half the width of the segment. *Styli* well developed, about three times as long as their greatest width, covered with numerous short hairs, armed at apical end with one short and one well developed seta. Below small seta and about half way up from base of stylus there is a well developed seta, which is somewhat smaller than large apical seta. This seta is lacking on more anterior styli, and occasionally is not to be found on some of the more posterior ones. *Calicles* from which the posterior sensory setae (trichobothria) arise surrounded with branched setae. *Cerci* about three and two-tenths times as long as their greatest width, well covered with moderately short setae, the terminal area small and facing outward. *Coxal sacs* located at bases of third to tenth pair of legs inclusive. *Length* four and two-tenths to five and five-tenths mm.

Holotype No. 5195. Calif. Acad. Sci. Ent. Calveras Dam, Alameda County, California, April 27, 1939. Described from numerous specimens collected on a hillside covered with a growth of native shrubs and trees. Specimens have also been taken at Woodacre in Marin County and on tree covered hills near Lagunitas. Specimens were found rather abundant in the soil a few inches below the leaf mold. The species has also been taken in the hills back of Vichy Springs in Napa County. It is apparently widely distributed in the uncultivated region surrounding the San Francisco Bay. It appears to prefer tree covered slopes and up to the present time it has never been taken in a cultivated region.

Scutigerella inculta is very distinctive. The long lateral setae of the fourth scutum distinguishes it from all the other known members of the genus. It has relatively long setae on the scuta as compared to other species, and has relatively few marginal and sub-marginal setae on the scuta, a character similar to that found in *S. linsleyi*. The erect setae on the outer surface of the tibia and tarsus are also characteristic, although a similar condition is found in *S. immaculata*, *S. palmonii* and *S. nodicercus*. *S. inculta* is closely related to *S. nodicercus* and the most important characters for the separation of the two are given under the description of the latter species.

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THE AMERICAN COMMISSION ON SCIENTIFIC NOMENCLATURE IN ENTOMOLOGY

The disturbed condition of the world during the last few years has interfered with the activities of the International Commission on Zoological Nomenclature and there is no prospect that this Commission will again function successfully for several years to come. Entomologists in the United States have felt that this situation should not be allowed entirely to stifle progress in the development of nomenclature and the clarification of nomenclatorial problems. At the meetings of the Entomological Society of America and the American Association of Economic Entomologists in San Francisco, in December, 1941, a plan was adopted which called for the establishment of an American Commission on Scientific Nomenclature in Entomology.

In accord with the terms of this plan, Mr. C. F. W. Muesebeck and Professor G. F. Ferris were appointed to organize the Commission. That organization has now been completed and the Commission is ready to function. It includes Prof. J. C. Bradley, of Cornell University; Mr. W. J. Brown and Mr. G. Stuart Walley, of the Division of Entomology of the Department of Agriculture of Canada; Prof. G. F. Ferris, of Stanford University; Prof. T. H. Hubbell, of the University of Florida; Prof. H. B. Hungerford, of the University of Kansas; Dr. E. G. Linsley, of the University of California; Prof. Clarence E. Mickel, of the University of Minnesota; Mr. C. F. W. Muesebeck and Mr. P. W. Oman, of the United States Bureau of Entomology and Plant Quarantine; Prof. A. G. Richards, Jr., of the University of Pennsylvania; Dr. Herbert H. Ross, of the State Natural History Survey of Illinois; Prof. C. W. Sabrosky, of the State Agricultural College of Michigan; Dr. R. L. Usinger, of the College of Agriculture of California. Prof. G. F. Ferris has been elected as Chairman.

The Commission will receive, consider and advise upon such nomenclatorial problems as are presented to it. All acts of the Commission will be in harmony with the International Rules of Zoological Nomenclature, although recommendations for the clarification, extension and improvement of these rules may be made. The Commission will report to the two parent societies at their next annual meeting. Communications concerning matters within the province of the Commission may be addressed to any of its members.—E. N. C.

NOTES ON TABANIDAE (DIPT.) FROM PANAMA

IX. THE GENERA STENOTABANUS LUTZ, LEPISELAGA MACQUART AND RELATED GENERA[1, 2]

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The group here treated includes five genera. Of these, *Stenotabanus*, *Lepiselaga* and *Diachlorus* appear to form a more or less related group. Such forms as *Diachlorus paradoxus* Lutz show many characters linking it with *Lepiselaga*, while *Stenotabanus calvitius* n. sp. is also quite *Lepiselaga*-like in a number of ways. *Selasoma* is much like a giant *Lepiselaga*, but there are a number of rather fundamental characters separating them, while *Bolbodimyia* still appears to have no close relatives.

Genus **Selasoma** Macquart

1838, Dipt. Exot., I, part 2, p. 187 (Type *Tabanus tibialis* Fab.). Surcouf, 1921, Gen. Insect., Fasc. 175, Dipt., Taban., p. 45. Lutz, 1913, Mem. Inst. Osw. Cruz, V, 2, p. 178. Enderlein, 1922, Mitt. Mus. Berlin, X, 2, p. 346; 1925, Op. cit., XI, 2, p. 352. Krōber, 1929, Enc. Ent., Ser. B, II, Dipt., V, pp. 104, 142. Borgmeier, 1933, Rev. Ent., III, p. 301. Krōber, 1934, Rev. Ent., IV, 2, p. 253.

Three species are placed by Krōber (1934) in this genus, *tibiale* Fab., *giganteum* Lutz and *nigrocaeruleum* Rond. Of these, *giganteum* seems only known from the types, which had no third antennal segment, and the species has not been subsequently recognized. *Nigrocaeruleum* has also not been taken since described, while the original description states that the antennae have a long dorsal spine. I suspect, therefore, that the species is very doubtfully assignable to *Selasoma*, and is more likely some species of *Dicladocera*, perhaps near *riveti* Surc.

The genus is not very clearly related to any others, but seems nearest *Lepiselaga*.

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[1]Part VI, these Annals, September, 1941, Parts VII and VIII, June, 1942.

[2]Printing costs paid by Gorgas Memorial Institute of Tropical and Preventative Medicine, Inc.

Selasoma tibiale Fabricius

(Figs. 1, 1a, 1b)

Tabanus tibialis Fabricius, 1805, Syst. Antl., p. 102 (no sex; America merid.). Wiedemann, 1821, Dipt. Exot., I, p. 89; 1828, Auss. Zweifl. Insekten, I, p. 164 (♀; South America). Von Röder, 1892, Wien Ent. Zeit., XI, 8, p. 237 (♀; Brazil).

Selasoma tibiale Macquart, 1838, Dipt. Exot., I, 2, p. 188 (♀; au nord de la capitainerie de Goyaz). Walker, 1854, List Dipt. Brit. Mus., Part V, Suppl. 1, p. 273. Kertesz, 1900, Cat. Taban., p. 28. Surcouf and Gonzalez-Rincones, 1912, Dipt. Vuln. Venezuela, II, p. 36. Lutz, 1913, Mem. Inst. Osw. Cruz, V, 2, p. 179, Pl. 13, fig. 21 (♀; Venezuela and Brasilian states of Rio de Janeiro, Sao Paulo, Minas Geraes, Goyaz, Bahia and Ceará). Ricardo, 1904, Ann. Mag. Nat. Hist., XIV, (7), p. 354. Surcouf, 1921, Gen. Insect., Fasc. 175, p. 47, Pl. 2, figs. 10a, 10b (Bresil). Kröber, 1929, Enc. Ent., Ser. B, II, Dipt., V, pp. 104, 142; Pl. 1, fig. 9; Pl. 3, figs. 48, 49, 62, 67; Pl. 4, figs. 94, 96, 97 (♂, ♀; Matto Grosso, Bolivia, Argentina, Brazil); 1934, Rev. Ent., IV, 2, p. 253.

Hadrus chalybaeum Perty, 1833, Del. Anim. art. Brasil, p. 183, Pl. 36, fig. 20 (Brasil).

Hadrus cyaneum Walker, 1848, List Dipt. Brit. Mus., V, Suppl. 1, p. 208.

Tabanus cyaneum Wiedemann, 1828, Auss. Zweifl. Insekt., I, p. 152. Macquart, 1838, Dipt. Exot., I, 2, p. 188. Walker, 1848, List Dipt. Brit. Mus., V, Suppl. 1, p. 273.

The species is easily separated from anything found in Panama by the basally black wings, shiny blue black abdomen, swollen tibiae, and the wide, flattened nearly toothless third antennal segment. The capture of this species here represents a very considerable extension of the known range, but comparison of Brazilian material with my two specimens has not revealed any important differences.

Distribution: Northern Argentina, Bolivia, Brasil, Venezuela and Panama.

Panama records: 2 ♀, Moja Pollo, Chagres River region, Jan. 19 and 31, 1940.

Genus **Lepiselaga** Macquart

1838, Dipt. Exot., I, 1, p. 153. Bequaert, 1924, Psyche, XXXI, 1, p. 26. Enderlein, 1925, Mitt. Mus. Berlin, XI, 2, p. 342. Borgmeier, 1933, Rev. Ent., IV, 2, p. 252. (Type, *Haematopota crassipes* Fab., 1805.)

Hadrus Perty, 1833, Del. Anim. Artic. Brasil, p. 183 (not *Hadrus* Dejean, 1833. Coleoptera).

Lepidoselaga Osten Sacken, 1876, Mem. Boston Soc. Nat. Hist., II, p. 435. Lutz, 1913, Mem. Inst. Osw. Cruz, V, 2, p. 30 (uses both *Lepiselaga* and *Lepidoselaga*). Krober, 1929, Enc. Ent., Ser. B, II, Diptera, V, p. 136.

But three species of this well marked and strictly Neotropical genus are known, and but one of these, the very widespread *L. crassipes* Fab., occurs in Panama. *Lepiselaga* does not appear to be very closely related to any other *Tabaninae*, but comes nearest *Selasoma*, *Diachlorus* and *Stenotabanus*.

The Genus may be characterized as follows: Small flies, seldom if ever reaching 10 mm. in length. Eyes bare, purplish black with green bands. Frons broad, without ocelli or vertexal tubercle. Frontal callus

well developed. Subcallus and facial area shiny and rather protuberant. Antennae with first two segments subcylindrical, the first 2 to 4 times as long as the second, the second about as long as wide. Third segment slender, the basal part subcylindrical or with a weak angle above, the terminal part of 4 annuli, which are sometimes nearly fused. Basal part at least twice length of annulate part. Palpi exceedingly broad and flattened, convex outwardly, flattened or concave inwardly, shiny. Proboscis short, shorter than head height, the labella mostly membranous, but with a small shiny plate near the base, about half length of proboscis. Thorax and abdomen, especially the latter, rather short and stout. Legs short and heavy, all tibiae markedly incrassate. Wings with subepaulet bare, costa, subcosta, and first vein with macrotrichia above, only costa and subcosta spinose beneath. All cells but anal open, no appendix on third vein. Wing black to the apex of discal cell or a little beyond, the apex and a triangular area in the region of the fifth posterior cell hyaline. Male (of *crassipes*) with palpi even larger and shinier than female, fronto-clypeus pollinose, reduced, and sunk between the greatly inflated genae. Eyes holoptic, bare, the large facets not greatly differentiated occupying about two-thirds eye area, and extending to the occipital margin. No tubercle between eyes at vertex.

Lepiselaga crassipes (Fabricius)

(Figs. 2, 2a, 2b)

Haematopota crassipes Fabricius, 1805, Syst. Antl., p. 108 (no sex; South America).
Lepiselaga crassipes J. Bequaert, 1926, Medical Rept. Harvard Exp. Amazon, p. 225 (with full synonymy). Kröber, 1934, Rev. de Entomologia, IV, p. 253. Van Volkenberg, 1939, Puerto Rico Agric. Expt. Sta., Circ. 22, p. 4. Bequaert, 1940, Rev. Ent., XI, 1–2, p. 285 (Cuba, Hispaniola, Puerto Rico); 1938, Carnegie Inst. Washington, Publ. No. 499, p. 226 (Guatemala). Fairchild, 1940, Psyche, XLVII, 1, p. 8, Pl. II, figs. 1–5 (early stages).
Tabanus lepidotus Wiedemann, 1828, Aussereurop. Zweifl. Ins., I, p. 193 (female; Brazil).
Lepiselaga lepidota Jaennicke, 1867, Abh. Senckenberg Naturf. Ges., 6, p. 312. Hine, 1910, Ohio Naturalist, X, 6, p. 149. Lutz, 1928, Est. Zool. Parasit. Venezolanas, pp. 56, 59, Pl. 9, fig. 2. Dunn, 1934, Psyche, XLI, 3, p. 172.
Lepidoselaga lepidota Loew, 1869, Berlin. Ent. Zeitschr., XIII, p. 6. Gowdey, 1926, Dept. Agric. Jamaica, Ent. Bull. 4, pts. 1–2, p. 76. Hine, 1910, Ohio Naturalist, X, 6, p. 149. Lutz, 1928, Ent. Zool. Parasit. Venezolanas, pp. 56, 59, Pl. 9, fig. 2. Dunn, 1934, Psyche, XLI, 3, p. 172.
Lepidoselaga recta Loew, 1869, Berlin. Ent. Zeitschr., XIII, p. 6 (♀; "New Granada"=Colombia).
Lepidoselaga major Szilády, 1926, Biologica Hungarica, I, pt. 7, p. 21 (♂, ♀; Santiago de las Vegas, Cuba).
Lepidoselaga crassipes Dunn, 1929, Am. Journ. Trop. Med., IX, 6, p. 502 (Colombia). Kröber, 1929, Enc. Ent., Ser. B. II, Diptera, V, p. 137, Pl. I, fig. 12; Pl. II, figs. 15, 45; Pl. III, fig. 61.

There seems no point in repeating the numerous references to this species in the literature, which have been adequately listed by Bequaert (1926). Only those subsequent to that date and the essential original citations are here included.

Freshly emerged specimens are striking insects, the frons, thorax, and most of the abdomen being covered with brilliant

irridescent golden green scales. The second abdominal tergite is black at the sides, only a broad median triangle bearing the green scales. In the male, these scales are much less abundant, nearly lacking on thorax and base of abdomen. The species is fairly abundant in Panama, but seldom sufficiently so to be very annoying. I am informed that it was much more plentiful formerly, and the reduction in numbers may be due to the great reduction in the water lettuce (*Pistia stratiotes*) in Gatun Lake which has taken place for unknown reasons in recent years, as that plant appears to be the favored larval habitat.

Distribution: Practically the whole Neotropical region, from Cuba and Southern Mexico to Ecuador, Paraguay and Northern Argentina.

Panama records: Numerous records from the Canal Zone region to Chiriqui in practically all months of the year. No records of the species from Darien Province, though it undoubtedly occurs there.

Genus **Bolbodimyia** Bigot

1892, Wien. Ent. Zeit., XI, p. 162 (Monotypic for *B. bicolor* Big., 1892, Venezuela). Kertész, 1900, Cat. Taban., p. 28. Hine, 1910, Ohio Naturalist, X, 6, p. 150. Enderlein, 1925, Mitt. Mus. Berlin, XI, 2, p. 341. Kröber, 1929, Enc. Ent., Ser. B, II, Diptera, V, pp. 109–112 and figs.; 1934, Rev. Ent., IV, 2, p. 257. Stone, 1934, Rev. Ent., IV, 2, p. 190; 1938, U. S. Dept. Agric. Misc. Publ. No. 305, p. 10.

Snowiellus Hine, 1904, Ohio Naturalist, V, 2, p. 230 (Monotypic for *S. atratus* Hine); 1910, Op. cit., X, 6, p. 151, figs. 1 and 5. Williston, 1908, Manual N. Amer. Dipt., p. 181, fig. 65. Enderlein, 1925, Mitt. Mus. Berlin, XI, 2, p. 353, (in part).

Five species are included by Kröber (1934) in his catalogue, and Stone (1938) transfers *Snowiellus atratus* Hine, a North American species, to the genus. The Neotropical species seem to be distinguished mainly on the relative amounts of orange and black coloration. I lack material for any definite conclusion, but it seems very possible that most, if not all, of these

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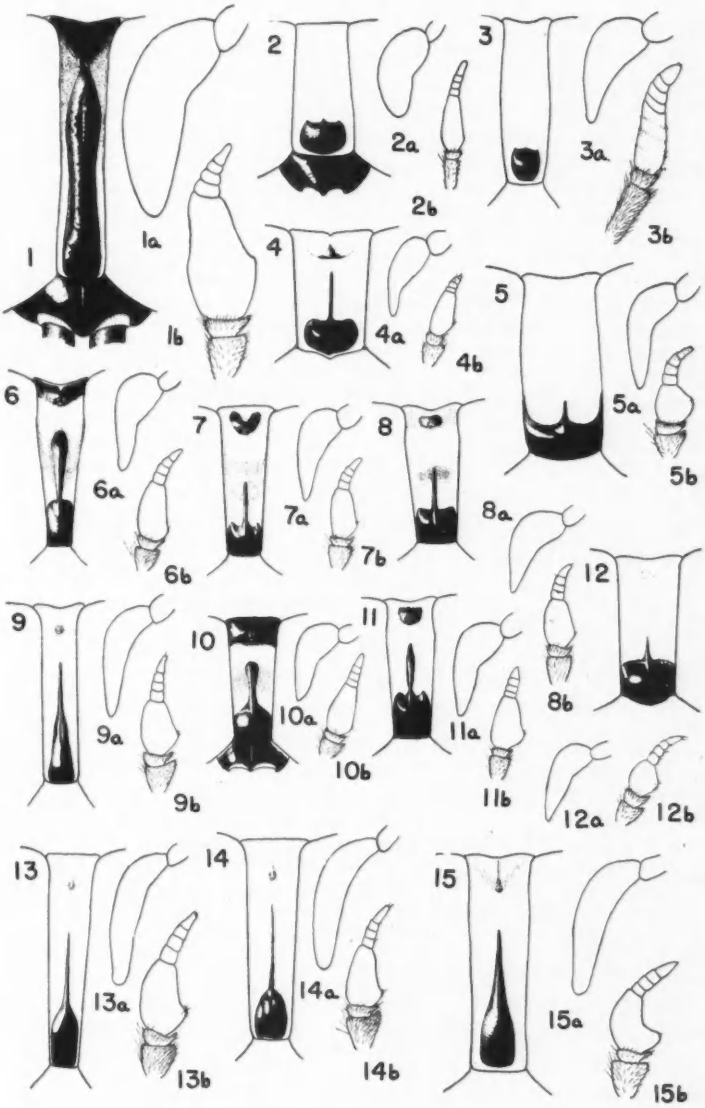
Explanation of Plate I

All figures are of the frons, palpus, and antenna of female specimens, and are all drawn to the same scale. All figured specimens are from Panamá.

Figs. 1, 1a, 1b, *Selasoma tibiale* (Fab.). Figs. 2, 2a, 2b, *Lepiselaga crassipes* (Fab.). Figs. 3, 3a, 3b, *Diachlorus curvipes* (Fab.). Figs. 4, 4a, 4b, *Stenotabanus longipennis* Kröb. Figs. 5, 5a, 5b, *St. changuinolae* sp. nov. Holotype. Figs. 6, 6a, 6b, *St. constabulorum* sp. nov. Holotype. Figs. 7, 7a, 7b, *St. minusculus* (Kröb.). Figs. 8, 8a, 8b, *St. maculifrons* (Hine). Figs. 9, 9a, 9b, *St. jaculator* sp. nov. Holotype. Figs. 10, 10a, 10b, *St. calvitius* sp. nov. Holotype. Figs. 11, 11a, 11b, *St. fulvistriatus* (Hine). Figs. 12, 12a, 12b, *St. paitillensis* sp. nov. Holotype. Figs. 13, 13a, 13b, *St. pequeniensis* sp. nov. Holotype. Figs. 14, 14a, 14b, *St. lerida* sp. nov. Holotype. Figs. 15, 15a, 15b, *St. plenus* (Hine).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forms are color variants of one and the same species. Six female specimens before me, from Aurá, Pará, Brasil, and Isla de Marajo, Pará, Brasil (R. Damasceno) have the palpi black, the fronto clypeus and genae orange, the thoracic pleura and sternum orange, and a faint orange ventral middorsal stripe on the abdomen. Otherwise the whole insect is black, including the legs. Another specimen, from Restrepo, Dept. Meta, Colombia (J. Bequaert coll.) has only the lower margins of genae and upper half of pleura orange.

The genus, based upon the material cited above, may be defined as follows: Eyes bare, dark purplish black, the lower two-thirds apparently rather finely and irregularly reticulated with green. Frons broad, narrowest at vertex, with basal and median calli, but no vertexal tubercle or vestiges of ocelli. Subcallus greatly inflated, shiny. Face and cheeks pollinose. First antennal segment greatly inflated, either subspherical or only inflated below; second segment short, not inflated, with or without a small dorsal tooth; third segment elongate, slender, the basal part as long or longer than the annulate part, with a dorsal angle very near the base; four annuli present. Palpi moderately slender, shorter than proboscis, the latter shorter than head height, the labium and labella mainly membranous, but with distinct shiny chitinized plates. Fronto-clypeus and genae pollinose, not inflated.

Wings with subepaulet bare, costa and first vein above, and costa and subcosta beneath with macrotrichia. All cells but anal open, no appendix on third vein, but the upper branch turned rather abruptly forward. Wing largely black or smoky. Legs with the tibiae, especially the fore pair, rather inflated. Small species, 12–14 mm. long, generally largely black in color, or with more or less orange or greyish pubescence on sides of body.

Only one species has been reported from Panama, and it is so far known only from the type specimen in the British Museum.

Bolbodimyia erythrocephala (Bigot)

Atylotus erythrocephalus Bigot, 1892, Mem. Soc. Zool. France, V, p. 668 (♀, Panama).
Tabanus erythrocephalus Kertész, 1900, Cat. Taban., p. 49; 1908, Cat. Dipt., III, p. 240. Surcouf, 1921, Gen. Insect., Taban., p. 67.
Bolbodimyia erythrocephala Kröber, 1929, Enc. Ent., Ser. B, II, Diptera, V, p. 112; 1930, Zool. Anzeiger, XC, p. 77, fig. 19 (♀; type); 1934, Rev. Ent. IV, 2, p. 258.

Kröber (1930) has redescribed and figured the type specimen, which has a yellow subcallus and antennae, white beard, and wholly black body with basally white mid and hind tarsi. So far as I know, the species has not since been taken.

Distribution: Panama.

Panama records: Only the original specimen.

Genus **Diachlorus** Osten Sacken

1876, Mem. Boston Soc. Nat. Hist., II, Pt. 4, No. 4, p. 47. Kertész, 1900, Cat. Taban., p. 29. Ricardo, 1904, Ann. Mag. Nat. Hist., (7) XIV, p. 356. Coquillett, 1910, Proc. U. S. Nat. Mus., XXXVII, No. 1719, p. 532 (Type, *Tabanus bicinctus* Fab., 1805). Lutz, 1913, Mem. Inst. Osw. Cruz., V, 2, 144. Surcouf, 1921, Gen. Insect., Taban., p. 49. Bequaert, 1924, Psyche, XXXI, 1, p. 38. Enderlein, 1922, Mitt. Mus. Berlin, X, 2, p. 349 (Type, *Chrysops ferrugatus* Fab., 1805); 1925, Op. cit., XI, 2, p. 336. Kröber, 1928, Beihefte z. Arch. f. Schiffs-u. Tropen-Hyg., XXXII, Beih. 2, p. 97. Borgmeier, 1933, Rev. Ent., III, 3, p. 290. Kröber, 1934, Rev. Ent., IV, 2, p. 255. Stone, 1938, U. S. Dept. Agric., Misc. Publ. No. 305, p. 13.

Dibasis Macquart, 1834, Hist. Nat. Dipt., V, 1, p. 207. (Type, *Tabanus bicinctus* Fab.). (Not *Diabasis* Hoffmansegg, 1819, Coleoptera.)

According to Kröber's catalogue (1934), this genus contains 23 species and one variety, of which all but three are confined to South America. *D. curvipes* Fab. extends into Central America, while *D. ferrugatus* Fab. ranges from Central America north into the southern United States. *D. badia* Kröb. is described as coming from "Georgia," but Kröber himself expressed skepticism as to the locality label. The same author has listed (1934, p. 263), *Stibasoma fulvohirtum*, a strictly Neotropical form, from "Georgia" also. In the material from Panama before me, there appear to be two species, *D. curvipes* Fab. and another, which Major Dunn had labelled *D. conspicuus* Lutz. It does not entirely agree with that species, of which I have specimens compared with the types, nor with any other described species, and is herein described as new.

The genus may be characterized as follows, based largely on Panama material:

Eyes bare, purple with a variable and often complicated pattern of green lines or spots. Frons broad to narrow, no ocelli or vertexal tubercle. Fronto-clypeus often more or less inflated and shiny. Antennae with the first segment always at least twice as long as the second, generally longer, often somewhat inflated. Second segment as long as wide, the two together at least half the length of the third segment. Third segment of a basal part and four annuli, the basal part is generally equal to or longer than the annulate part, obscurely annulated, and frequently with a blunt dorsal angle. Palpi markedly inflated, as long as proboscis. Proboscis shorter than head height, the fleshy labella more than half total length of proboscis.

Thorax and abdomen unremarkable, much as in *Tabanus*. Legs rather short and stout, the fore tibiae generally more or less inflated and often darker than the other legs. Wings with subepaulet bare, costa, first longitudinal (R1) and at least basal part of fifth vein (Cu) with macrotrichia above; beneath, both costa and subcosta bear macrotrichia. Wings hyaline, with or without costal apical or subapical dark markings. Size small, seldom if ever exceeding 12 mm.

The two Panama species of Diachlorus may be separated as follows:

1. Frons parallel sided, the frontal callus slender, considerably higher than wide. Last two abdominal segments black and wholly black haired. . **jobbinsi**
2. Frons widest in the middle, the frontal callus nearly square. Last two abdominal segments with yellow hairs in the middle. . . . . **curvipes**

Diachlorus jobbinsi sp. nov.

Female—Length 8–10 mm., of wing, 7.5–9 mm.

Frons yellow-pollinose, 5.5 to 6 times as high as basal width, parallel sided. Frontal callus brown, narrower than frons, twice as high as wide and with a slender prolongation above. Fronto-clypeus black, shiny. Genae yellowish grey pollinose. Antennae yellow, the terminal annuli dusky. Palpi yellow, moderately inflated. Thorax mostly yellow pollinose. Mesonotum with a thick, dark trident-shaped figure in the middle, the prongs pointing anteriorly, and a pair of dark isolated shoulder spots. Pleura and sternum between fore and mid legs pearly, otherwise yellow pollinose. Scutellum dark at base, the apex yellow. Legs with all coxae and femora yellow, fore tibiae and tarsi black and black haired, mid tibiae and tarsi yellow, whitish at bases, hind tibiae yellow with some dark hairs, the tarsi whitish at base. Wings hyaline, tinged with yellow in the costal area, and with a black apical spot which includes the whole apex beyond the fork of the third vein, from the costa to the fourth vein (M_1), with sometimes a faint infuscation in the apex of the second posterior cell. Abdomen yellow, first tergite and a broad median stripe from second to fifth tergites yellow haired, otherwise black haired; the two terminal tergites black and black haired. Beneath, the vestiture is wholly yellow, except for the two terminal sternites.

Holotype ♀ and 2 ♀ Paratypes, El Real, Darien Province, Panama, March 20, 1941; 1 ♀ Paratype, El Real, Darien, Feb. 7, 1940 (D. M. Jobbins coll.); 3 ♀ Paratypes, Yape, Darien Province, Panama, Jan. 25, 1940 (D. M. Jobbins coll.).

This species is very close to *curvipes*, but may be distinguished from it by slightly narrower and parallel sided frons, more slender callus, slenderer palpi, black terminal segments of the abdomen, and the presence of dark shoulder spots and absence of median yellow stripe on the mesonotum. From *conspicuus* Lutz it may be distinguished by the yellow margined scutellum, paler legs, and less extensive dark apex to the wing. The species flies in company with *curvipes*, but appears to be less abundant.

Diachlorus curvipes (Fabricius)

(Figs. 3, 3a, 3b)

Haematopota curvipes Fabricius, 1805, Syst. Antl., p. 107 (South America).
Tabanus curvipes Wiedemann, 1821, Dipt. Exot., I, p. 90; 1828, Aussereurop. Zweifl. Ins., I, p. 176 (♀).
Diabasis curvipes Macquart, 1834, Hist. Nat. Ins. Dipt., I, p. 208 (♀). Walker, 1854, List Dipt. Brit. Mus., V, p. 271.

Diachlorus curvipes Williston, 1895, Kansas Univ. Quart., III, 3, p. 193 (♀). Hunter, 1901, Trans. Amer. Ent. Soc., XXVII, p. 138. Ricardo, 1904, Ann. Mag. Nat. Hist. (7) XIV, pp. 358 and 359 (♀). Bréthes, 1907, An. Mus. Nac. Buenos Aires, XVI, p. 284. Kertész, 1908, Cat. Dipt., III, p. 211. Ad. Lutz, 1907, Centralbl. Bakt. Parasitenk., Abt. I, XLIV, p. 142; 1913, Mem. Inst. Osw. Cruz, V, pp. 145 and 189, Pl. XII, fig. 1 (♀). Neiva and Penna, 1916, Op. cit., VIII, p. 94. Bodkin and Cleare, 1916, Bull. Ent. Research, VII, p. 185. Surcouf, 1921, Gen. Insect., Taban., p. 51.

Chrysops afflictus Wiedemann, 1828, Aussereurop. Zweifl. Ins., I, p. 204 (♀; Brazil). Walker, 1854, List Dipt. Brit. Mus., V, p. 288. Hunter, 1900, Trans. Amer. Ent. Soc., XXVII, p. 135. Ricardo, 1904, Ann. Mag. Nat. Hist. (7) VIII, pp. 310 and 313. Kertész, 1908, Cat. Dipt., III, p. 181. Surcouf, 1921, Gen. Insect., Taban., p. 150.

Diachlorus (?) *afflictus* Ad. Lutz, Mem. Inst. Osw. Cruz, V, pp. 163 and 189.

?*Diabasis ataenia* Macquart, 1838, Dipt. Exot., I, p. 152 (in part; specimens from Pará). Walker, 1854, List Dipt. Brit. Mus., V, p. 271.

Chrysops varipes Walker, 1854, List Dipt. Brit. Mus., V, p. 289 (♀; Pará). Hunter, 1901, Trans. Amer. Ent. Soc., XXVII, p. 145.

Diabasis varipes Rondani, 1848, in Baudi and Truqui, Studi Entom., I, p. 105 (no sex; Brazil), (p. 45 of reprint).

Diachlorus varipes Hunter, 1901, Trans. Amer. Ent. Soc., XXVII, p. 138. Ricardo, 1904, Ann. Mag. Nat. Hist. (7) XIV, p. 359. Kertész, 1908, Cat. Dipt., III, p. 213. Surcouf, 1921, Gen. Insect., Taban., p. 51. Enderlein, 1925, Mitt. Mus. Berlin, XI, 2, p. 336. Bequaert, 1926, Med. Rep. Harvard Exp. Amazons, Pt. II, p. 223 (Pará; Panama). Kröber, 1928, Beih. z. Arch. f. Schiffs-u. Trop.-Hyg., XXII, 2, pp. 8, 43, fig. 19 (♀; French Guiana; Pará; Iquitos); 1934, Rev. Ent., IV, 2, p. 256.

This species does not appear to be very abundant in Panama, except about the Rio Tuira in Darien Province, where most of my material has come from. It attacks man readily, like other species of the genus.

Distribution: Recorded in the literature from Panama, Venezuela, British and French Guiana, Brazil (States of Pará, Amazonas, Bahia, Sao Paulo), and Paraguay. Dr. Bequaert took the species at Muzo, Dept. Boyaca, Colombia.

Panama records: El Real, Darien Prov., Aug. 11 to 30, 1930 (H. C. Clark coll.; det. Kröber); Jan. 24 and Feb. 7, 8, and 10, 1940 (D. M. Jobbins coll.). Chepigana, Darien Prov., July 22, 1931 (L. H. Dunn coll.). Pihuila, Darien Prov., March 27, 1933 (L. H. Dunn coll.). Margarita Is., near Ft. Randolph, C. Z., June 30 (J. B. Shropshire coll.). Pacora, March 26, 1939. Moja Pollo, Chagres River region, July 23, 1940. Mt. Hope, C. Z., Oct. 30, 1939.

Genus **Stenotabanus** Lutz

1913, Brasil Medico, No. 45, p. 6 (reprint), Dec. 1. (Defined in key, no species); 1914, Mem. Inst. Osw. Cruz, VI, 3, p. 167 (reprinting of 1913 paper); 1922, Zoologia Medica, Publ. Sep. da "Folha Medica," Rio de Janeiro, pp. 9 and 11 (in key, no species). Lutz and Neiva, 1914, Mem. Inst. Osw. Cruz, VI, 2, pp. 73, 74 (*St. taeniotes* Wied. in list of species). Bequaert, 1924, Psyche, XXXI, 1, p. 30 (Type, *Tabanus taeniotes* Wied.). Enderlein, 1925, Mitt. Mus. Berlin, XI, 2, p. 354 (Type *T. taeniodes* (!) Wied., equals Lutz' genus only in that it includes *taeniotes*). Kröber, 1929, Enc. Ent., Dipt., V, p. 113; 1934,

Rev. Ent., IV, 2, p. 258 (with 20 Neotropical species). Borgmeier, 1933, Rev. Ent., III, 3, p. 301 (with *Styposelaga* End. as synonym). Stone, 1938, U. S. Dept. Agric., Misc. Pub. No. 305, p. 31 (7 Nearctic species). Bequaert, 1940, Rev. Ent., XI, 1–2, p. 289 (Subgenus of *Tabanus*, 15 Antillean species). Philip, 1941, Can. Ent., LXXIII, pp. 10, 11, 14.

Myiotabanus Lutz, 1928, Est. Zool. Parasit. Venezolanas, p. 58, Pl. 8, fig. 4. (Monotypic for *M. sarcophagoides* n. sp.). Kröber, 1934, Rev. Ent., IV, 2, p. 275 =*Leucotabanus*).

Styposelaga Enderlein, 1925, Mitt. Mus. Berlin, XI, 2, p. 342 (Monotypic for *St. sexannulata* End.).

This genus as here understood includes a considerable number of mostly small flies with the general facies of *Tabanus*. Structurally the genus is quite heterogeneous, and it will eventually be necessary to divide it into more homogeneous groups, but for the present only two of the more obvious forms will be tentatively assigned sub-generic standing.

The genus in the broad sense may be defined as follows: Eyes bare, at least in the female, with or without green or purple bands. Frons medium to very broad, frontal callus present, median and vertexal calli present or absent. Antennae *Tabanus*-like, the tooth on the third segment usually short, rarely prominent, often absent. Annulate portion of third segment usually with 4 annuli, but with a tendency to reduction to 3 or rarely 2 annuli. Proboscis generally short, the labella large and membranous. Wings with all cells but anal open, with or without an appendix on the third vein. Subepaulet typically without macrotrichia but in a few species discussed below, hairs are present to a variable extent. Legs as in *Tabanus*. Thorax as in *Tabanus*, sometimes with iridescent scale-like hairs. Abdomen very variously ornamented.

KEY TO SUBGENERA

1. Frons broad, not more than three and one-half times as high as wide, frontal callus variable, generally wider than high and as wide as frons. Vertexal tubercle absent, rarely a small denuded vertexal area present. Antennae with four well marked annuli.....subg. **Aegialomyia** Philip
   Frons narrow or very broad, frontal callus variable. Vertexal tubercle present, or at least a denuded shiny area at vertex. Antennae variable.... 2
2. Frons relatively narrow, generally at least five times as high as wide. Vertexal tubercle well marked, often with vestiges of ocelli. Antennae with four well marked annuli.....subg. **Stenotabanus** Lutz
   Frons very broad, hardly twice as high as wide, callus transverse, narrower than frons. Vertexal area with a small shiny spot. Fronto-clypeus with a deep, denuded, pit on each side. Antennae with but three well marked annuli, the terminal annulus a small button, or fused with the preceding annulus.....subg. (nov.) **Brachytabanus**

Subgenus **Aegialomyia** Philip

1941, Can. Ent., LXXIII, p. 10. (Type *T. psammophilus* O. S.).

Although Philip established the present group as a full genus, I prefer to treat it subgenerically until the Neotropical forms become better known.

The group as here understood includes a number of very

broad fronted species which for the most part seem confined to a sea beach or coastal marsh environment.

In addition to the characters given in the key, these species are distinguished by the generally pale coloration, pale legs, often spotted wings, multiple banded eyes, short to very short proboscis, short, stubby antennae, with disproportionately thickened terminal annuli, and abdominal pattern, when present, of a median and lateral row of pale spots on darker ground.

I consider the following described species to belong to this group: *T. psammophilus* O. S., *T. atlanticus* Johns., *T. nervosus* Curran, *T. caribaeorum* Bequaert, *T. laevicallus* Szilády, *T. jamaicensis* Newstead, and *T. magnicallus* Stone. The males, known for *psammophilus*, *caribaeorum*, *atlanticus*, *nervosus* and *magnicallus* have the eyes bare, the large facets very extensive and sharply differentiated and demarkated from the small facets, and there is no vertexal tubercle. Two species of the group occur in Panama, both apparently undescribed, and each represented by but a single female specimen.

Stenotabanus (Aegialomyia) paitillensis sp. nov.

(Figs. 12, 12a, 12b)

Female—Length 8 mm., of wing 7 mm. Eyes bare, in life with the upper and lower margins broadly purple, the broad green median area crossed by two narrow purple bands set close together, or the eye may be said to be purple with two broad and one narrow green band. Frons as figured, brownish grey pollinose, the frontal callus mahogany brown, markedly protuberant, vertexal area a little denuded, but without a definite callus or tubercle. Subcallus and facial area brownish above, grey beneath, the beard white. Antennae as figured, yellowish throughout. Palpi as figured, white with dark and light hairs mixed.

Mesonotum and scutellum pale brown, the former with two very faint stripes. Pleura grey, whitish haired. Legs uniformly pale brown, the fore tibiae faintly dusky at apex. Wings hyaline, upper branch of third vein with a rather long appendix. Abdomen pale brown, the tergites broadly grey behind, and with a mid-dorsal row of grey triangles. There is also a dorsolateral row of rounded grey spots broadly joined to the hind marginal band.

Holotype ♀, Paitilla Airport, Panama, March 19, 1941, to be deposited in the M. C. Z., Harvard Univ., Cambridge, Mass.

This little species appears to be related to *littoreus* Hine, and *campechianus* Towns. From the first of these it may be distinguished by smaller size, differently marked eyes and abdomen, broader antennae, and wholly pale legs, and from the latter by abdominal pattern.

Stenotabanus (Aegialomyia) changuinolae sp. nov.
(Figs. 5, 5a, 5b)

Female—Length 12 mm., of wing 11 mm. Eyes bare, the pattern not revivable. Frons as figured, brownish grey, the callus mahogany brown. Antennae as figured, brown, the hairs on first two segments black. Subcallus and face pale brown; beard sparse, whitish. Palpi as figured, pale brown, mostly pale haired. Proboscis hardly longer than palpi, brownish.

Mesonotum and scutellum cocoa brown, with four fairly prominent paler stripes. Pleura concolorous. Legs wholly brown, mostly white haired. Wings very dirty, but apparently hyaline with very small clouds on at least the distal cross veins. Fork of third vein with a short appendix. Abdomen somewhat crushed, but apparently uniformly pale brown.

Holotype ♀, Changuinola Dist., Bocas del Toro Prov., Panama (L. L. Pechuman leg.). The species seems quite closely related to *laevicallus* Szil. and *jamaicensis* Newst., but the frons is even broader, the third antennal segment considerably wider, and the size larger. The specimen is not in the best condition, so that fresh material will be necessary to define its relationships with the West Indian species more clearly.

Subgenus **Brachytabanus** subg. nov.

I am creating this name for the reception of *Stenotabanus longipennis* Kröber, which seems to me to be sufficiently distinct from other *Stenotabanus* known to warrant separation.

The subgenus may be defined as follows: Female eyes bare, green with three narrow purple bands in life. Frons very broad, less than twice as high as wide. Frontal callus wider than high, very convex. Vertexal tubercle represented by a broadly crescentic transverse ridge, with a small bare area above it. Subcallus pollinose, without hairs. Anterior tentorial pits greatly enlarged, black and shiny within. Third antennal segment with basal part longer than wide, dorsal angle very obtuse. Annulate portion with a tendency to reduction, so that there are often but three visible annuli, the fourth being very small and more or less fused with the third. Wings rather long and narrow, with macrotrichia on the costa, subcosta and first vein above, and with a very short appendix or none.

Stenotabanus (Brachytabanus) longipennis Kröber
(Figs. 4, 4a, 4b)

Stenotabanus longipennis Kröber, 1929, Enc. Ent., Ser. B, Dipt., V, p. 125, Pl. I, fig. 23; Pl. II, figs. 7, 37; Pl. III, fig. 55 (♀; Venezuela); 1934, Rev. Ent., IV, 2, p. 258.

This peculiar little species does not seem to be very closely related to any species with which I am familier. The antennae

are reminiscent of *Microtabanus pygmaeus* Will., but there the similarity stops. Kröber's description and figures are excellent, but omit one character which seems peculiar to this species.

On each side of the clypeus are two grooves, the anterior tentorial pits of Snodgrass, which in many Tabanids have a tendency to form rounded pits at their lower ends, but in this species these pits are greatly enlarged and shiny black within, so that they appear as round, black spots or holes on each side of the otherwise greyish pollinose face. The whole insect is light brown, the legs yellowish, the abdomen with a broad creamy haired mid-dorsal stripe, on each side of which the abdomen is blackish haired to about the same width as the stripe, the sides of the tergites being again broadly light haired. The wings seem unusually long and narrow.

Distribution: Venezuela, Colombia and Panama. A specimen before me labelled Venezuela, Nov., 1936 (Anduze), agrees perfectly with Panama material, while there is a series of 14 ♀ from Muzo and Villavicencio, Colombia, in Dr. J. Bequaert's collection.

Panama records: 1 ♀, Gamboa, C. Z., July 9, 1924 (N. Banks); 2 ♀, Utevey, near Pacora, Aug. 6, 1941, on horse.

Subgenus **Stenotabanus**

This group includes a large number of small species with relatively narrow frons, usually well developed vertexal tubercle, and often a dark hair patch in the position of the median callus. The group includes *T. taeniotes* Wied. (the Genotype), *T. fulvistriatus* Hine, *T. maculifrons* Hine, *T. flavidus* Hine and probably a considerable number of other species, though further study of actual material will be necessary before placing most of them.

St. plenus Hine belongs to a group of species including *St. tantulus* Hine, *muscoideus* Hine and *sarcophagoides* Lutz. They are characterized by a narrow club-shaped callus, wholly dark legs, and eyes with a single green band or none. The species all bear a striking superficial resemblance to Muscoid or Sarcophagid flies. If further study of the group shows the advisability of separation, the name *Myiotabanus* Lutz is available, though as only one species occurs in Panama, it seems best to leave it in *Stenotabanus* for the time being.

The eight remaining species before me from Panama fall into two rather distinct groups. *Fulvistriatus, minusculus, maculifrons, constabulorum* and *calvitius* are all small species with a more or less extensive shiny vertexal area surrounding

the tubercle, a callus as wide as the frons, usually with a dark hair patch in the middle of the frons, and with unmarked wings.

Lerida, jaculator and *pequeniensis* are without the shiny vertexal area or mid-frontal hair patch, the callus is narrower than frons, and the wings are spotted. This last group is rather anomalous, as all three species may have hairs on the subepaulet. *Lerida* usually has this structure bare, but may have from one to three strong macrotrichia, *pequeniensis* nearly always has a few macrotrichia, up to 12 on a side, while in *jaculator* macrotrichia are abundant, though more sparse than on the adjoining costa. It is with some trepidation that these species are retained in *Stenotabanus*. They might with almost equal justification be considered an aberrant group of *Tabanus*. The characteristic wing pattern, the well marked vertexal tubercle bearing vestiges of ocelli, and the general habitus seem to me to place them somewhat closer to such species as *St. parvulus* Will. and *St. brunettii* Beq., which have bare subepaulets, than to *lucidulus* Walk. which Bequaert places in *Macrocormus*. The latter has a very similar wing pattern, but lacks a vertexal tubercle and the subepaulets bear macrotrichia. The use of the subepaulet in Tabanid classification has proven very useful, but this is one case where it seems to confuse rather than clarify. It would be quite impossible to place these species correctly in Philip's (1941) key to Nearctic Tribes and Genera, as any placement would allocate the obviously closely related species into different Tribes, and even in some cases necessitate the placing of different specimens of the same species in different categories. Although it is important to call attention to such cases, it seems foolish to abandon the subepaulet character on the grounds that it will not always work. The fact that intermediate forms exist is in reality a valuable clue to phylogenetic relationships.

KEY TO FEMALES

1. Frontal callus narrower than frons. A vertexal tubercle, but no denuded patch at vertex. Palpi rather slender, not markedly inflated basally..... 2
   Frontal callus as wide as frons. A shiny area of variable extent surrounding vertexal tubercle. Palpi markedly inflated basally..... 5
2. Stout thickset species. The thorax black with four prominent grey stripes, abdomen black with the first two tergites with whitish bloom, 2nd to 6th tergites with whitish hind margins and yellow haired median triangles. Legs black. Wings hyaline and with a small dark area from stigma to apex of second basal cell. Basal part of third antennal segment broad, and with a strong dorsal angle..... **plenus**
   Slender species, the thorax unstriped, wings with cross veins clouded, and antennae without a strong dorsal angle..... 3

3. Abdomen light brown, a black median tegumentary spot on second tergite, and all tergites prominently pale margined behind. Wing faintly smoky, all veins narrowly brown margined and strong clouds on all cross veins and fork of third vein. Appendix long. . . . . **lerida**
Abdomen immaculate, or with faint pale hind marginal bands. Wings smoky mainly apically and along fore border. Veins not brown margined. . 4
4. Frons distinctly convergent below. Wings heavily fumose apically. Third vein with a moderate to long appendix. . . . . **pequeniensis**
Frons parallel sided. Wings lightly fumose along fore border. Third vein without an appendix. . . . . **jaculator**
5. Wings markedly fumose along fore border. Abdomen light brown with a broad creamy mid-dorsal stripe from scutellum to apex. Frons without median dark hair patch. Legs largely yellow. . . . . **fulvistriatus**
Wings entirely hyaline. Abdomen black or dark brown, without a median stripe. Frons always with at least a small median black hair patch. Legs largely black. 6
6. Thorax prominently striped. Scutellum dark with a wide pale border. All tergites prominently pale margined behind. . . . . **minusculus**
Thorax unicolorous or with golden or greenish hairs, not striped. At least the first tergite dark. 7
7. Thorax and abdomen entirely blackish above. Tergites narrowly and faintly pale behind, but without pale hairs. Frons narrow and convergent, the callus nearly twice as high as wide. . . . . **constabulorum**
Thorax and abdomen with pale hairs. Tergites prominently pale and pale-haired behind. Frons broader, the callus as wide as high. 8
8. Subcallus denuded and shiny. Whole vertex black, denuded and shiny. Scutellum and third to sixth tergites densely golden haired behind. . **calvitius**
Subcallus pollinose. Vertex with but a small denuded area surrounding tubercle. Scutellum without dense golden pilosity. Tergites two to six with narrow whitish hind marginal bands. . . . . **maculifrons**

Stenotabanus (Stenotabanus) fulvistriatus (Hine)

(Figs. 11, 11a, 11b)

Tabanus fulvistriatus Hine, 1912, Ohio Naturalist, XII, 7, p. 515 (♀; Chiapas, Mexico). Surcouf, 1921, Gen. Insect., Taban., p. 69. Kröber, 1934, Rev. Ent., IV, 3, p. 309 (not seen).
Tabanus unistriatus Dunn, 1934 Psyche, XLX, 3, p. 174 (in part).

There are two specimens in the Hine collection, one labelled "Dona Maria, Chiapas (Crawford)" and "Type," the other from Higuito, San Mateo, Costa Rica. The type has slightly broader antennae and a slightly narrower frons. Material from Panama which I compared with these specimens agrees best with the Costa Rica specimen. The species is exceedingly close to *taeniotes* Wied., of which I have specimens from Southern Brazil. The only differences I can discover are the more brownish wings of *fulvistriatus*, the more slender antennae of *taeniotes* and the presence in the latter of very narrow light hind margins to the tergite. *St. peruviensis* Kröb. and *St. pallidicornis* Kröb. from Peru and Bolivia also seem very close.

Distribution: Southern Mexico, Costa Rica, Panama.

Panama records: 3 ♀, Puerto Armuelles, Chiriqui Prov., July 27, 1929 (L. H. Dunn; det. as *unistriatus* Hine).

Stenotabanus (Stenotabanus) maculifrons (Hine)

(Figs. 8, 8a, 8b)

Tabanus maculifrons Hine, 1907, Ohio Naturalist, VIII, 2, p. 222 (♀; Puerto Barrios, Guatemala). Surcouf, 1921, Gen. Insect., Taban., p. 74. Kröber, 1934, Rev. Ent., IV, 3, p. 311 (not recognized).

The types in the Hine collection consist of 2 ♀, Puerto Barrios, Guatemala, March 4 and 7, 1905. My material consists of 1 ♀ from Chilibre, Madden Highway, Panama, Jan. 1, 1940, and 1 ♀, Restrepo, Dept. Meta, Colombia (Antunes coll.), and differs in no way from the types. The Colombian specimen was determined for me in 1936 as *St. sexannulatus* End. by Dr. G. M. de Oliveira Castro. The species are certainly exceedingly close, but Kröber's figures (Op. cit., 1934, p. 122 and figs.) show a rather narrower and more convergent frons for *sexannulatus*. Since I have seen no specimens from anywhere near the type locality (Bolivia) it seems best to keep the two separate for the present.

Distribution: Guatemala, Panama and Colombia.

Panama records: Only the single female referred to, which was taken on the screens of a house.

Stenotabanus (Stenotabanus) constabulorum sp. nov.

(Figs. 6, 6a, 6b)

Female—Length 8.5 mm., of wing 8 mm. Eyes bare, purple with two narrow green bands in life. Frons as figured, yellowish grey pollinose, with a large black haired median area. Subcallus and face yellowish grey, beard greyish. Antennae as figured, dark reddish, the apical half of third segment blackish. Palpi as figured, brownish, mostly black haired. Proboscis short, hardly longer than palpi, dark brown.

Mesonotum and scutellum black, unstriped, sparsely grey pollinose, and with sparse brassy scale-like hairs. Pleura yellowish grey and creamy haired above, steel grey below. Legs with coxae and femora black, fore tibiae half, posterior tibiae three-fourths white basally, otherwise black. Tarsi black. Wings hyaline, the costal cell and basal area faintly yellowish. There is a short appendix on the third vein. Abdomen black, the tergites very narrowly reddish behind, and bearing a small tuft of yellowish hairs in the middle and extreme sides. Venter greyish pollinose, all sternites whitish, and white haired behind.

Holotype ♀, Police Station, Pequeni River, Madden Lake, C. Z., May 11, 1940.

This species agrees quite well with Kröber's description of his *St. obscurus*, except that the frons is entirely different, being 8 instead of 3½ times as high as wide, and definitely convergent.

Named in honor of the Canal Zone Police force, whose hospitality has afforded me the opportunity for much valuable collecting.

Stenotabanus (Stenotabanus) minusculus (Kröber)

(Figs. 7, 7a, 7b)

Pseudocanthocera (?) *minuscula* Kröber, 1930, Zool. Anz., XC, 3–4, pp. 80–81, fig. 21 (♀; Vulcan Colima, Mexico); 1934, Rev. Ent., IV, 2, p. 260.

A series of specimens before me from Panama agree in most respects with Kröber's description and figure. My material differs, however, in the white or partly white tibiae, a character not mentioned by Kröber. The species has little or nothing in common with *Ps. sylveirii* Macq., the genotype. I give below a description of the Panama material for comparison with Kröber.

Female—Length 7–8 mm., of wing 7 mm. Eyes bare, purple with two narrow green bands in life. Frons as figured, yellowish grey with an extensive median dark patch. Callus and bare vertexal area black. Subcallus and face yellowish grey, beard yellowish. Antennae as figured, dull yellowish brown, the annulate portion darker. Palpi as figured, yellowish brown, mostly white haired. Proboscis but little longer than palpi, blackish.

Mesonotum blackish brown, with two wide dorsal stripes and the lateral margins yellowish pollinose, the whole with scattered dark and brassy hairs. Scutellum black, broadly yellowish grey margined behind. Pleura yellowish grey, darker below, yellow haired and with a brown dark haired stripe extending forward from the wing bases. Legs variable, the femora black to yellowish brown, black haired, the fore tibiae bicolored, white basally, black apically; posterior tibiae largely white and pale haired. Tarsi dark. Wings hyaline, with or without a short appendix. Abdomen black, or with the anterior tergites partly or wholly cinnamon brown. First, and to some extent the second, tergites with a grey bloom; all tergites conspicuously yellowish or whitish on hind margins, and with pale hairs. These transverse bands may be slightly wider in the middle, but do not form distinct triangles. The band on the first tergite is narrower than the others. Sternites grey pollinose, the hind margins whitish. The striped thorax of this species will distinguish it from *maculifrons* Hine. Kröber's *obscurus* also appears to be close, but the thorax is unicolorous.

Panama records: 2 ♀, Juan Mina Station, Chagres River region, C. Z., Feb. 8 and March 9, 1939; 2 ♀, Moja Pollo, Chagres River region, Feb. 16, 1940; 1 ♀, Pacora, March 26, 1939; 1 ♀, El Real, Darien Province, Feb. 8, 1940; 1 ♀, Darien (Dunn).

Stenotabanus (Stenotabanus) plenus (Hine)

(Figs. 15, 15a, 15b)

Tabanus plenus Hine, 1907, Ohio Naturalist, VIII, 2, p. 225 (♀; Izabal, Guatemala). Surcouf, 1921, Gen. Insect., p. 79. Krōber, 1934, Rev. Ent., IV, 3, p. 313.

The types in the Hine Collection consist of 6 ♀ from Izabal, March 7, 1907, in fair condition. The abdomens are somewhat reddish at base. There are also 5 ♀ from Higuito, San Mateo, Costa Rica (Schild coll.) in the Hine collection. Hine's description is good, but may be supplemented in a few details. A small though definite tubercle is situated in a small bare area on the vertex. The abdomen bears median dorsal triangles of light hairs, and the tergal hind marginal fringes mentioned by Hine may be continuous or interrupted on each side of the median triangles. I have also seen 1 ♀, Guatemala City and 1 ♀, El Rancho, both Guatemala, in Coll. Bequaert.

Distribution: Guatemala, Costa Rica, Panama.

Panama records: Porto Bello, Feb. 24, 1911 (Busck), El Valle, Cocle Prov., April 13, 1941. Moja Pollo, Chagres River region, Jan. 11, 1941.

Stenotabanus (Stenotabanus) calvitius sp. nov.

(Figs. 10, 10a, 10b)

Female—Length 8 mm., of wing 6.5 mm. Frons about three and one-half times as high as basal width, rather convergent, grey pollinose with a wide transverse band of black pollinosity in the region of the median callus. The frons is also rather well covered by long decumbent hairs. Basal callus black, as wide as frons, about as wide as high, broadly joined to the inverted club-shaped median callus. Vertexal tubercle well marked with vestiges of three yellowish ocelli. Whole vertex to below tubercle denuded, shiny black. Subcallus denuded, black and shiny, with but a narrow grey pollinose strip along eye margins. Eyes bare under a hand lens, but showing sparse and scattered hairs under higher power. Eyes in life purple, the upper and lower margins dark green, and with two fairly broad golden-green median transverse bands. Fronto-clypeus and genae grey pollinose, the latter with a pale straw colored beard. Antennae dark reddish throughout, the first two segments with black hairs. Palpi blackish, thinly grey pollinose, and with abundant and long pale yellow hairs, and shorter black hairs. Proboscis about one-half longer than palpi, black, the labella more than half its length, fleshy.

Mesonotum black, thinly dark grey pollinose, fairly well covered with greenish golden iridescent hairs. Scutellum densely clothed with long bright golden hairs. Pleura dark grey, with sparsely grey hairs. Wings hyaline, the stigma black, no appendix on fork of third vein. Legs black, the basal half of fore tibiae white and white haired, the mid and hind tibiae wholly white, except extreme apices, and the

mid and hind basitarsus also white, or yellowish. First two tergites black and black haired, except at extreme postero lateral angles, which are yellow haired. Tergites 3 to 5 with pale pollinose and yellow haired hind marginal bands, widened in the middle and at the sides. Sternites dark grey pollinose, all with pale haired hind marginal bands.

Holotype ♀, Panama City, Republic of Panama, Jan. 10, 1942. Taken on windows of automobile. To be deposited in the Museum of Comparative Zoology.

This little species seems closest to *maculifrons* Hine and *sexannulatus* End. It differs from the former in its more brilliant coloring and lack of a pale hind marginal band on the second tergite and from the latter by its heavily golden haired scutellum and lack of anything approaching a series of connected mid-dorsal triangles on the abdomen. From both species it differs in having a bare subcallus and the whole vertex bare and shiny.

Stenotabanus (Stenotabanus) lerida sp. nov.

(Figs. 14, 14a, 14b)

Female—Length 10–11.5 mm., of wing 10.5–11 mm. Eyes bare, apparently green with a single purple band in life. Frons a little over five times as high as basal width, slightly narrowed below, yellowish brown pollinose. Frontal callus dark brown, higher than wide, narrower than frons, and prolonged in a slender line two-thirds the distance to the vertex. Vertexal tubercle present, and with traces of three ocelli. Subcallus yellowish pollinose, with sparse long whitish hairs. Frontoclypeus and genae grey, sparsely greyish haired. First two antennal segments yellowish, black and pale haired. Basal part of third segment orange, longer than wide, the dorsal tooth small and near base. Annulate portion black, shorter than basal portion. Palpi pale brownish, slender, mostly black haired. Proboscis brown, but little longer than palpi; the labella membranous, large, over half length of proboscis.

Mesonotum and scutellum brown, indistinctly greyish striped and with sparse golden hairs. Pleura, sternum and coxae grey pollinose, rather abundantly grey haired. Legs light brown, the tarsi and apices of fore tibiae darker. Femora pale haired, tibiae and tarsi mostly dark haired. Wings with subepaulet bare, but with macrotrichia upon costa, subcosta and first and fifth veins above, costa and subcosta beneath. Wings faintly smoky, darker along costa and hind margin, and with prominent clouds on all cross veins. Upper branch of third vein long appendiculate, costal cell yellow. Abdomen orange brown, darker towards apex, the hind margins of all tergites paler and yellow haired, rest of tergites dark haired. The second tergite, and rarely the third, bears a median black integumental spot. Venter pale reddish brown, mostly pale haired.

Holotype ♀ and 7 ♀ Paratypes, Boquete, Chiriqui Province, Panama, March-April, 1941 (Mrs. T. B. Monniche coll.); 9 ♀

Paratypes, same locality, April, 1940 (Mrs. T. B. Monniche coll.); 1 ♀ Paratype, Cerro Punta, Chiriqui Province, Feb.-March, 1940, 6,000 ft. (T. T. Howard coll.).

This little species belongs to a rather widespread tropical American group including the West Indian *St. brunettii* Bequaert and *St. batesi* Bequaert and a considerable number of as yet unnamed continental species.

Stenotabanus (Stenotabanus) pequeniensis sp. nov.

(Figs. 13, 13a, 13b)

Female—Length 10–12 mm., of wing 9–10.5 mm. Eyes bare, uniformly green in life. Frons narrow, about six and one-half times as high as basal width, yellowish brown pollinose. Basal callus black, about twice as high as wide, nearly as wide as frons, and prolonged above in a slender line two-thirds the distance to the vertex. Vertexal tubercle present, small, but often with vestiges of ocelli. Subcallus orange brown pollinose. Fronto-clypeus and genae greyish pollinose, the latter with a sparse grey beard. Antennae yellowish brown, the terminal annuli darker. First and second segments not swollen, black haired. Basal part of third segment a little longer than annulate portion, and somewhat longer than broad. Dorsal angle moderate, with a tuft of black hairs. Palpi brownish, black haired, slender, nearly as long as antennae. Proboscis a little longer than palpi, brown, the labella about half length of proboscis, fleshy.

Mesonotum dark brown, dark haired, unstriped. Pleura and sternum greyish. Legs dark brown, the coxae greyish pollinose and grey haired. Subepaulet with macrotrichia, but much less densely hairy than costa. Costa, subcosta, first and basal part of fifth veins with macrotrichia above, costa and subcosta also hairy beneath. Upper fork of third vein with a short appendix. Whole wing fumose, but definitely darker along costa and at apex. Cross veins with small dark clouds. Abdomen yellowish brown, darker towards apex, black haired, rarely with faint indications of yellowish mid-dorsal triangles. Venter paler, with pale hairs.

Holotype ♀, Rio Pequeni, Madden Lake, Panama, Aug. 21, 1941; 2 ♀ Paratypes, same data; 1 Paratype, Rio Pequeni, May 11, 1940; 1 ♀ Paratype, Moja Pollo, Chagres River region, C. Z., May 15, 1940; 4 ♀ Paratypes, Cerro Azul, near Pacora, Panama, May 17, 1940; 3 ♀ Paratypes, Meta, Colombia (in coll. J. Bequaert). Holotype and 3 Paratypes to be deposited in the M. C. Z., Harvard University, Cambridge, Mass.

This little species appears to be related to *T. lucidulus* Walker of Jamaica, for which Bequaert (1940) uses the subgeneric name *Macrocormus*, and from which it differs in

unmarked abdomen and more slender palpi. *T. modicus* Hine, from British Guiana, appears also to be close, but is considerably darker and with slightly different frons and antennae. I have seen Hine's unique type.

Stenotabanus (Stenotabanus) jaculator sp. nov.

(Figs. 9, 9a, 9b)

Female—Length 8–10 mm., of wing 9–9.5 mm. Eyes bare, the color pattern not revivable in the material at hand. Frons medium, about five times as high as basal width, parellel sided, steel grey pollinose. Frontal callus black, slightly narrower than frons, square below, about twice as high as wide and merging gradually into a slender line which reaches two-thirds of the distance to the vertex. Vertexal tubercle small, but distinct, with vestiges of ocelli. Subcallus, fronto-clypeus and genae pale grey pollinose, only the last two with sparse pale hairs. First two antennal segments pale yellowish, slightly inflated, black haired. Basal part of third segment orange, longer than wide, longer than annulate portion, and with an obtuse non-salient dorsal angle. Annulate portion somewhat dusky. Palpi pale brown, black haired, rather slender and not acutely pointed. Proboscis brownish, the fleshy labella over one-half its length.

Mesonotum pale reddish brown, grey pollinose. Pleura, sternum and coxae grey pollinose. Legs rather uniformly pale brown. Wings above with subepaulet, costa and first vein with macrotrichia, subcosta with a few hairs in the middle section, fifth vein wholly bare. Wings smoky, especially along the costa, and all cross veins with small clouds. Abdomen pale reddish brown, without apparent markings.

Holotype ♀ and 1 ♀ Paratype, Bohio, C. Z. (A. H. Jennings); 2 ♀ Paratypes, Las Cascadas, C. Z. (A. H. Jennings).

All of the types are old and somewhat rubbed, but the species is quite distinct on frontal characters. It comes nearest *pequeniensis*, but is smaller, paler throughout, and has a broader, more parallel sided frons. Some of these specimens were labelled *parallelus* Wlk., but although the resemblance is great, that species has a bare subepaulet, and a quite different frons.

THE RELATION OF THE PREY OF SPHECIUS SPECIOSUS TO THE SIZE AND SEX OF THE ADULT WASP

(Hym.: Sphecidae)

RICHARD DOW,
Reading, Mass.

It has frequently been observed that the female cicada killer, *Sphecius speciosus* (Drury), provisions each cell of her nest with one or two cicadas. As the sexes of the adult wasp show a considerable difference in average size, the male being much smaller, it is natural to ask: does the sex of an adult bear any relation to the amount of prey with which its cell was provided? In other words, are the sex and size of the adult wasp directly correlated with the number and weight of the stored cicadas? Though I am far from reaching any final answers, it seemed worth while to put my present results on record, especially as they suggest one or more promising lines of investigation which I have no immediate prospect of being able to follow.

SEX OF ADULT WASP AND NUMBER OF STORED CICADAS

On August 28, 1937, in an area of coarse sandy soil in Berkley, Massachusetts, to which I was directed by Mr. N. S. Easton of Fall River, I excavated the contents of more than forty cells of *speciosus*. These cells were grouped in the vicinity of two burrows about a yard apart, but it is doubtful that they belonged to only two nests. In fact, I did not attempt to find them by tracing their connections, but having dug a fairly deep hole into which the loose dirt could fall, merely scraped away the sides of the pit. (This is a useful method even if one is excavating a burrow probed with the flexible stem of a plant.)

The larva of *Sphecius speciosus* differs from that of most aculeate wasps in leaving the exoskeleton of the prey practically intact. Consequently, from 42 cells, I was able to obtain the remains of 66 cicadas, partially dismembered, but in such condition that it was not only possible to tell the species and sexes involved but to give the exact contents of each cell. In the work of identifying this material, partly on the basis of the terminal segments of the female and the opercula of the

male, I received much help from Dr. Charles H. Blake. *Tibicen canicularis* (Harr.) was represented by 14 males and 27 females, and *T. lyricen* (Deg.) by 10 males and 17 females, a total of 24 males as against 44 females. This agrees with the observations of W. T. Davis (1921: 128), who says of the cicadas caught by the wasp: "The female *Sphecius* seeks them, not by the song of the males as is sometimes stated, but by flying carefully along the limbs of trees and up and down the trunks, and so catches both sexes. In some of the burrows dug out, there were many more females than males." The smaller number of male victims does not imply an irregular sex ratio in the cicadas. It might be that the females are less active (hence more susceptible to capture), longer lived (therefore more abundant during the nesting period of the wasp), or more likely to occur where the wasp will find them. There is also the possibility that there is some selection on the part of the wasp.

In 18 of the 42 cells mentioned above, I failed to discover any stage of the wasp, even empty cocoons. The rest contained cocoons which had been completed, at least externally. Two of these were broken accidentally in the process of excavation, but from the remaining 22, I subsequently reared 18 adults.

In two cells not otherwise considered in the present study, the remains of prey were associated with opened cocoons from which wasps had apparently emerged. Since *speciosus* has but one generation a year, this discovery indicates that the contents of a cell may persist in a recognizable state over at least one winter, and that some of the 18 cells without cocoons may have belonged to nests of other years. The importance of these details will become obvious in the discussion.

It was apparent, even while I was excavating the cells, that the cocoons were of two different classes in respect to size. Subsequent measurements of their length and weight showed that the two groups were quite distinct, and separated by intervals of 5.0 mm. and 1.0 g.

One of the most unexpected results of my observations was the discovery of two cells which apparently contained three cicadas, and though another was recorded in my field notes as having been stored with two specimens of the prey, the remains of three cicadas were later found in the material belonging to this cell. Unfortunately, none of these cells contained cocoons.

TABLE I

DATA PERTAINING TO THE CELLS FROM WHICH ADULTS WERE REARED

Number of cicadas in cell	1	1	1	1	1	1	1	1	1	1	2 ?	2	2	2	2	2	2	2
Tibicen canicularis	♂	♂	♂	♂	♀	♀	♀				♂, ♀	♂, ♀	♀, ♀	♀, ♀	♀	♀		
Tibicen lyricen								♂	♂	♀					♀	♀	♀, ♀	♀, ♀
Estimated weight of prey (g.)	0.93	0.93	0.93	0.93	1.12	1.12	1.12	1.39	1.39	1.94	2.05	2.05	2.24	2.24	3.06	3.06	3.89	3.89
Length of cocoon (mm.)	24.0	29.5	29.5	29.5	29.5	29.5	31.0	32.0	31.0	32.0	31.0	32.0	40.0	39.0	40.5	39.5	40.5	40.5
Weight of cocoon (g.)	0.67	1.05	1.30	1.25	1.14	1.28	1.37	1.39	1.59	1.48	1.30	1.62	2.96	2.96	3.40	3.16	3.15	3.33
Weight of adult (g.)	0.13	0.25	0.28	0.43	0.27	0.36	0.38	0.36	0.42	0.39	0.43	0.44	0.63	0.69	0.81	1.09	0.61	1.06
Sex of adult	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀

Of the remaining cells, 21 were definitely stored with one cicada, and 11 of these contained small cocoons from which I reared 10 males. Either 17 or 18 cells were stored with two cicadas, and 9 of these contained large cocoons from which I reared 6 females. The cell whose contents were doubtful in respect to the number of victims, and another which was certainly provisioned with two cicadas, each contained a cocoon that belonged to the smaller of the two classes and subsequently produced a male wasp. This shows that the number of victims stored in a cell was not perfectly correlated with the sex of the resulting wasp. (See figure 1 and table I.)

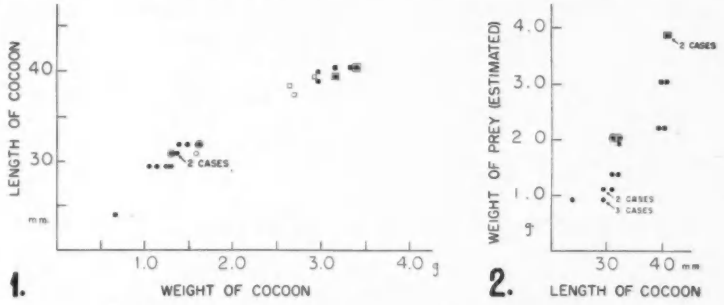


FIG. 1. Weight of cocoon plotted against length of cocoon.
FIG. 2. Length of cocoon plotted against estimated weight of prey.

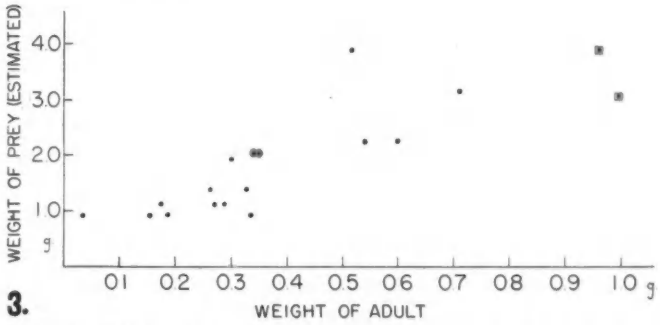
KEY TO SYMBOLS USED IN GRAPHS

Circular symbols represent data pertaining to cells which produced, or were likely to produce, males. *Square symbols* represent corresponding data for females. The ***plain circle*** and the ***plain squares*** refer to cocoons which failed to produce adults, or were prevented from doing so. The ***round dots inside circles*** represent data pertaining to the two cells which produced males but were provisioned with two cicadas (one case doubtful). The ***square dots inside squares*** represent data pertaining to the cells whose cocoons produced females with imperfect wings.

SIZE OF ADULT WASP AND WEIGHT OF STORED CICADAS

There remains for consideration the correlation of the total weight of the stored cicadas with the length of the cocoon and the weight of the adult wasp. As noted above, the larva of *Sphecius speciosus* leaves recognizable remains of the prey. On the other hand, without excavating the cells before the larva has begun to feed, there is no way of getting an accurate figure for the weight of the victims. Having no data of this sort, because of the season when my excavations were made, I obtained some freshly captured cicadas in 1938, and from the

weights of these specimens, estimated those of the prey stored the previous year. Though I had only two males and one female of *Tibicen canicularis*, and one male and two females of *T. lyricen*, it is apparent from figure 2 that the different combinations of the two species and two sexes of the cicadas give an evenly graded series of weights, and that there is no conspicuous break between the combinations of one and two cicadas, or between those in the cells which produced males and those in the cells which produced females. A still lighter combination of two cicadas, which was possible but did not occur in any of the 42 cells, was two males of *canicularis*. According to my figures, this would be somewhat lighter than a single female of *lyricen*.



3.

FIG. 3. Weight of adult plotted against estimated weight of prey. (See legend accompanying figs. 1 and 2.)

The relation between the weight of the reared adults and the estimated weight of the prey is shown in figure 3. In this graph the difference in weight of the two sexes of the wasp is in very obvious contrast to the uniform gradation in the weight of the prey. Whether additional data would show as clear-cut relationships is, of course, very doubtful.

A graph of the weight of the adults plotted against the length of the cocoons (figure 4) shows fairly good correlation, especially when allowance is made for the two heaviest females, both of which were specimens that failed to develop perfect wings.

On the whole it is surprising that the graphs are at all satisfactory. They are not only based on few data, but the measurements themselves are subject to criticism. In the

first place, aside from the fact that the actual victims could not be weighed, one may question the significance of the weight of the cicadas inasmuch as the larvae do not consume all of their prey. In the second place, the weight of a fresh cocoon is not necessarily an accurate index of the size of the pupa it contains, because the actual cocoon includes a large amount of inorganic material. In the third place, the present measurements of the adults are not too reliable because of the following factors: (1) Three or more of the cocoons had been opened for inspection. (2) The wasps were late in reaching maturity (August 8 to September 10, 1938), probably because of the necessarily artificial conditions under which they were reared. (3) The specimens were weighed both alive and dead varying periods of time after reaching complete development. (4) Two abnormal females are included.

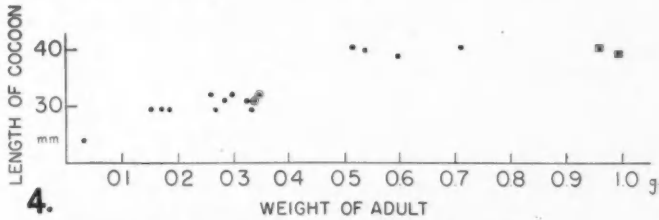


FIG. 4. Weight of adult plotted against length of cocoon. (See legend accompanying figs. 1 and 2.)

From the above results, however, two tentative conclusions may be drawn. First, the weight of the adult wasps was roughly proportional to that of the prey with which their cells were stored. Second, although the sexes of the reared adults formed two separate classes in respect to weight, there was no corresponding segregation in the estimated weights of the provisions.

DISCUSSION

The finding of a general agreement between the number of stored cicadas and the sex of the adult wasp was not particularly surprising in itself, nor does there seem to be any reason to believe that my records were abnormal. In fact, the possibility that such a situation might exist was suggested long ago by C. V. Riley (1892: 250), in the following statement: "In the cells containing two Cicadas the larva acquires

larger size, and as the female wasp is a good deal larger than the male, this should indicate that one Cicada only is required for the latter and two for the former, though I have no idea that the amount of nourishment influences the sex (a favorite theory with some naturalists) for I believe that sex is predetermined in the egg."

An experimental approach to this problem was tried in the summer of 1938. The procedure was to give an additional cicada to wasp larvae that had been provided with only one, and to take away from larvae with two cicadas the second victim. By this means, I hoped to discover the effect of increased and reduced amounts of prey. Unfortunately I did not have sufficient time for this work, and my few experiments ended in failure.

At first my own line of thought was to wonder if the quantity of stored food could have any influence on the sex of the wasp, or if there might be any mechanism whereby the female could either provision a cell with an amount of prey suited to the sex of the egg, or even lay an egg of the appropriate sex. Further consideration of my findings and the study of an interesting paper on the same general subject by W. B. Herms (1928) have made me very skeptical of the first hypothesis that the amount of food may affect the sex of the larva. An article by C. P. Clausen (1939) suggests that the second hypothesis is not out of the question.

Assuming that the sex of the wasp is finally determined in the egg, we might otherwise account for the relation between the quantity of stored prey and the sex of the adult wasp by postulating that female larvae with insufficient food fail to become adults, and that male larvae with an excess of food are likewise prevented from reaching maturity. Though it is difficult to imagine a mechanism which would produce this result in the males, and this hypothesis requires that with 50 percent general mortality each female would have to complete eight cells, nevertheless it is pertinent to recall the fact that in 18 out of 44 cells I found no cocoons. This suggests that future studies of the possible effect of food on sex, as well as the sex ratio, should take into account the mortality during development.

Dr. Charles H. Blake, whom I wish to thank for much valuable help and criticism in the course of this study, has suggested another hypothesis, namely, that the sex of the eggs

laid by the female in the course of the nesting period might change during this period (probably near the middle) at essentially the same time that the wasp begins to place a different quantity of prey in the cells. This could be readily studied by observational methods; the other hypotheses would be more difficult to test.

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Riley, C. V. 1892. The larger digger-wasp. Insect Life, 4: 248–252, figs. 32–38.

TEXTBOOK OF CLINICAL PARASITOLOGY, by DAVID L. BELDING. Pages xxi and 888, 279 figs., 4 col. pls., 7 x 10 inches. 1942. Published by D. APPLETON-CENTURY COMPANY, INC., 35 West 32nd Street, New York City. Price, postpaid, $8.50.

The present war has served to focus attention upon the need for control of parasitic diseases among civilian populations and the armed forces. The publication of Dr. Belding's Textbook of Clinical Parasitology is quite timely. In this book, the author has considered the subject of medical parasitology as a whole. The subject matter includes information on protozoan, helminthic and arthropod parasites of man, their diagnosis, pathology, treatment and control. Teachers of medical parasitology should find this authoritative text excellent for use by their classes. Likewise, physicians in civil practice, the armed forces, public health services and laboratory workers will find it fulfilling many of their practical needs.

The manufacture of the book is excellent and its organization shows painstaking care and foresight. The many diagramatic and semi-diagramatic figures are so constructed and arranged as to present to the reader a complete picture of the life cycle of each parasite, independent of the discussion. It departs from the traditional textbooks of parasitology by its method of presentation as well as the inclusion of chapters on immunity of parasitic infections and the diagnosis of parasitic diseases. Full treatment is accorded common cosmopolitan parasites and those peculiar to the Western Hemisphere. The uncommon or minor parasites are briefly mentioned in small type.

Keys separating major groups of parasites are supplemented, wherever possible, by tabulations of morphological data for comparison. At the end of each chapter is a list of references which are largely limited to publications in English. Citations to literature are carried as footnotes with authors' names and dates. One will find at the close of the discussion an excellent bibliography of books and journals appertaining to parasitology.

The section devoted to arthropods consists of 179 pages of discussion, figures, keys and tables of data. Emphasis is placed upon the biological aspects of parasitic arthropods rather than their morphology. This section thus includes an excellent review of the insects that are directly injurious to man himself. It is especially good because of the numerous diagramatic illustrations. In this part will be found an eight page table summarizing much of the information about arthropods which serve as vectors of human diseases.

This textbook is recommended to entomologists who desire an up-to-date source book on the parasites of man.—W. M. TIDD.

THE IMMATURE STAGES OF SOME MINNESOTA PLECOPTERA

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In recent years at the University of Minnesota attention has been directed toward the study of the immature forms of the orders of aquatic insects. Elkins (1936) began a study of the larvae of Trichoptera and Denning (1937) continued work on that group. Daggy (1938) began the study of the Ephemeroptera of the state, giving special attention to the immature forms of the order. This present study is an endeavor to further the knowledge of another aquatic group, the Plecoptera, found abundantly throughout the various types of streams of Minnesota. Four Plecoptera nymphs definitely associated with previously known species are treated in this study. Included also is a review of the methods of rearing and associating nymphs with adults.

Eleven species of stoneflies were recorded for Minnesota in Needham and Claassen's "Monograph of the Plecoptera or Stoneflies of America North of Mexico." Miscellaneous collecting over the state added to the number of stoneflies in the Minnesota collection of insects. Early in 1939 Dr. T. H. Frison, of the Illinois Natural History Survey, kindly determined these Plecoptera, finding a total of 32 species for the state in the collection. Of the species listed by Needham and Claassen for the state two are not represented in this collection. In addition 9 other species have been collected and determined by the writer. The total of Minnesota species is now 43. Of the 43 species recorded for Minnesota, the nymphs of 26 had been associated with the imago before this work was undertaken; the nymphs of four known species dealt with in this paper bring this number to 30.

A list of the Plecoptera of Minnesota, including those species determined by Frison, two species recorded by Needham and Claassen (1925) and not represented in the Minnesota collection, and species collected and determined by the writer, is as follows:

PTERONARCIDAE
Pteronarcys dorsata (Say)
Pteronarcys frigida Gerstäcker
Pteronarcys nobilis Hagen

TAENIOPTERYGIDAE
Taeniopteryx (*Brachyptera*) *glacialis* (Newport)
Taeniopteryx nivalis (Fitch)
Taeniopteryx parvula Banks
Strophopteryx fasciata (Burmeister)

NEMOURIDAE
Nemoura completa Walker
Nemoura rotunda Claassen
Nemoura trispinosa Claassen
Nemoura venosa Banks

LEUCTRIDAE
Leuctra decepta Claassen
Leuctra hamula Claassen

CAPNIIDAE
Capnia opis (Newman)
Allocapnia granulata (Claassen)
Allocapnia minima (Newport)
Allocapnia torontonensis Ricker

PERLIDAE
Atoperla ephyre (Newman)
Perlinella drymo (Newman)
Neoperla clymene (Newman)
Perlesta placida (Hagen)
Acroneuria abnormis (Newman)
Acroneuria internata (Walker)
Acroneuria lycorias (Newman)
Acroneuria ruralis (Hagen)
Neophasganophora capitata (Pictet)
Togoperla media (Walker)

PERLODIDAE
Isogenus frontalis Newman
Hydroperla varians (Walsh)

CHLOROPERLIDAE
Hastaperla brevis (Banks)
Hastaperla orpha (Frison)
Isoperla annecta (Needham and Claassen)
Isoperla bilineata (Say)
Isoperla longiseta Banks
Isoperla marlynia Needham and Claassen
Isoperla montana (Banks)
Isoperla richardsoni Frison
Isoperla signata (Banks)
Isoperla transmarina (Newman)
Isoperla truncata Frison
Isoperla sp. n. 1
Isoperla sp. n. 2
Alloperla imbecilla (Say)

The division into families is that of Frison (1935).

Various methods of associating nymph with adult have been used with work on stoneflies. Rearing is the most reliable. Smith, one of the pioneers in the work, describes her methods (1913: 203) as follows: "The essential factor in rearing stoneflies, as in many other stream-inhabiting insects, is running water. This is provided by a series of taps in a roof garden aquarium and also in a small artificial pond out of doors. . . . In the artificial pond the nymphs are kept, eight or ten together, in cylindrical cages made of galvanized wire screen with cheese cloth covers. The cages are partially submerged in the current near the taps. With flat stones and bits of water weed in the bottom, and a steady flow of water, the nymphs can live a natural life." Wu (1923) kept and reared his specimens in vials stopped with bolting silk and in small fine wire-screen cylinders placed in the bed of a small spring fed stream. Frison (1929) reared nymphs by keeping them in small tins containing moist leaves until the adults emerged. Frison later (1935) used another technique for rearing, that of putting the nymphs in cages of screen and wood and suspending these, part in water, from a specially built raft anchored in running water.

Claassen (1931) described another method of associating nymph with adult if the nymph is sufficiently mature, that of the recognition of the developing genitalia through the exuviae or with the exuviae "peeled off." Another possibility is that of collecting nymphs, exuviae, and adults at the time of emergence from a locality at which there is only one species emerging at the given time.

REARING TECHNIQUE

The method of rearing used in this work with stoneflies is essentially that used by Denning (1937) rearing Trichoptera and by Daggy (1938) rearing Ephemeroptera. In this method a series of air outlets is connected to a source of compressed air by means of rubber tubing and glass or metal "T" joints. From these outlets air is forced through "alundum" bacteriological filters into the water in small rearing jars about 20 cm. in diameter and 5 to 25 cm. deep. These alundum filters break up the air flow through the water into a stream of fine bubbles. This type of aeration simulates stream conditions quite well as shown by the effectiveness in maintaining individual stonefly nymphs for a long period. A screen cylinder around each jar with a piece of cheesecloth over it furnishes a surface on which emergence can take place and confinement for emerged adults.

A moisture trap and a reducing valve were installed between the main source of compressed air and the lead-off tubing to the apparatus described above. The moisture trap was primarily for the protection of the reducing valve from any water that might get into the compressed air line. The reducing valve made possible the regulation of air flow to the rearing jars. Since the pressure of the main line varied from 15 to 30 pounds per square inch, without a reducing valve difficulty was encountered in regulating the air flow to the filters without an occasional "blowout" with accompanying failure of the aeration of the system and often the loss of valuable specimens from lack of oxygen. The reducing valve used had a meter attached to further facilitate the regulation of the air pressure to the system; a two pound pressure from the reducing valve was found to be most effective.

Such a system has been in operation continuously for sixteen months without mishap. One *Pteronarcys* nymph, collected in August, 1939, emerged in December of the same year, a period of four months in one of these rearing jars. Another *Pteronarcys* nymph, collected in April, 1940, emerged January, 1941; this is a period of nine months.

To maintain a lower than room temperature for the rearing of early spring species, some of the rearing jars were set in running faucet water to about the level of the water in the jars. By this means a temperature of about 10 degrees C. was maintained.

DESCRIPTIONS OF SPECIES REARED

Taeniopteryx (Brachyptera) glacialis (Newport)

(Figs. 3, 5, 6, 7 and 8)

1848 *Nemoura (Brachyptera) glacialis* Newport. Proc. Linn. Soc., London 1: 389.
1851 *Nemoura (Brachyptera) glacialis* Newport. Trans. Linn. Soc., London 20: 450.
1861 *Taeniopterynx glacialis* Hagen. Synopsis of Neuroptera of N. A., p. 36.
1928 *Taeniopteryx glacialis* Claassen. Ann. Ent. Soc. Am. 21: 667.
1929 *Brachyptera glacialis* Frison. Ill. Nat. Hist. Sur. Bull. 18: 373.
1938 *Taeniopteryx glacialis* Ricker. Trans. Roy. Canad. Inst. 22: 131.

Male nymph.—General color brownish black with legs, cerci, wing-pads, antennae, and clypeus brownish yellow. Antennae and cerci very long. Length of body 10 mm.; segments in antennae 96 to 100; length of antennae 10 mm.; segments in cerci 64; length of cerci 11 mm.

Head somewhat narrower than pronotum; supra-antennal plates prominent with a slight outcurving above each antenna and a more acute outcurving ahead of each antenna; lateral ocelli just back of a line connecting the anterior margin of the compound eyes; the distance between the lateral ocelli is three times the distance from one to a compound eye; base of the ocellar triangle slightly longer than one of the sides. Color of head dark brown with anterior spot between antennae and posterior part of supra-antennal plates brownish yellow; rugosities present between compound eyes on the caudal portion of the head; dorsal part of enlarged basal segment of each antenna dark brown; the rest of each antenna brownish yellow; antennae about as long as the body.

Pronotum one-third wider than long; posterior and lateral margins only slightly convexed; anterior margin very convex; lateral and anterior margins brownish yellow; disc brown with darker rugosities. Forewing pads very short, their inner margins almost in a straight line with the margin of the mesonotum. Rearwing pads longer and rather acute.

Anterior half of each abdominal segment darker than posterior half. Row of setae present on the posterior of each segment with scattered setae throughout each segment. Dorso-caudal lobe of the 10th segment of the male nymph is dark brown and shows the developing supra-anal plate in more mature specimens. Dark brown embossings show on the lateral aspects of tergites 1 through 8.

Legs brownish yellow, darker toward extremities. Each femur with a notch in its distal margin. Each tibia with two spines on its distal margin. Row of long silky hairs on outer margin of legs. Second tarsal segment longer than first; first and second together as long as the third. Cerci slightly longer than body.

Total ventral aspect yellow except as follows: a brown longitudinal line on each side in the cervical region; a brown blotch on each coxa and on each trochanter; a brown median "T" on the mesosternum, a crosswise line on the metasternum, and an increasingly dark brown color from the 8th abdominal sternite caudally.

Ventral median lobe of 9th abdominal sternite with its sides evenly curved, extending past the end of the abdomen, and with its length two times its width.

DISCUSSION

This was one of the American species of stoneflies omitted from Needham and Claassen's monograph on the Plecoptera of North America and listed under the following statement by Claaassen (1928): "The following are species unable to be recognized because of inadequate descriptions, loss of type material, or inaccessibility to types." The latter phrase probably applied to this species since Ricker (1938) did examine the original cotypes in the British Museum, figured, and redescribed them. The types of this species were from Nova Scotia. No date of collection was mentioned either by Newport in his original description or by Ricker. However, Newport does give the general time of appearance in the following statement (1851: 451), "It appears in the spring (end of March or beginning of April), when the ice becomes honeycombed, and even before then, and at the same time as the preceding species (*Capnia vernalis*), but is not so numerous."

Specimens of this species, determined as such by Frison in 1939, were collected by Daggy and Chalgren from the ice along the Stewart River, Lake County, Minnesota, March 26, 1938. At the same time four nymphs were taken by Daggy from the stream itself. Stewart River is one of the small swift rocky streams that flow into Lake Superior from the north.

Nemoura trispinosa Claassen

(Figs. 4, 9, 10, 11 and 12)

1923 *Nemoura trispinosa* Claassen. Canad. Ent. 55: 289.
1925 *Nemoura trispinosa* Needham and Claassen. Monograph of the Plecoptera of North America, p. 213.

Female nymph.—General color yellowish brown with pronotum darker than abdomen and head darker than pronotum. No gills of any kind evident. Head and pronotum the same width. Length of body 7 mm.; segments of antennae 55; segments of cerci 25; width of head 1.32 mm.; width of pronotum 1.32 mm.; length of pronotum 0.9 mm.; distance between hind ocelli 0.45 mm.; distance from hind ocellus to eye 0.12 mm.

Head almost uniformly dark except for sutures and lateral tubercles. Arms of the epicranial suture somewhat sinuate midway on each. Lateral ocelli barely visible at the curves of the lateral arms. Longitudinal rugosities posterior to the arms of the epicranial suture.

Pronotum with width one and one-third times the length; front margin almost straight; front angles rounded; hind angles very broadly rounded, so much so that the lateral margins and posterior margin make an approximate half circle; a row of stout setae on the anterior and lateral margins, and across the posterior somewhat ahead of the

Fig. 2. Nymph of *Isoperla transmarina*.

Fig. 1. Nymph of *Isoperla annecta*.

margin, being more sparsely scattered across the posterior; four small round dark spots on each half of the pronotum with other shadowy markings about them.

Front wing pads four times as long as broad; hind wing pads four-fifths as long as front ones and one-third wider; anal lobe of hind wing pad about two-thirds the total length of its inner margin. A band of setae across the anterior margins of both mesonotum and metanotum; more numerous at the ends of each band.

Legs dull yellow, covered with fairly stout setae except for naked areas as follows: most of the anterior surface of the fore femora, a longitudinal line on the anterior surface of each of the other femora and of each tibia, the posterior surface of the caudal pair of femora, and a longitudinal line on the ventral surface of each femur and each tibia. No line of silky hairs present on the outer margin. First and second tarsal segments together about as long as the third; second very short.

Abdomen yellowish brown above with the anterior margin of each segment lined with dark brown; anterior margins of tergites 5 through 7 slightly emarginate; posterior margin of each tergite lined with setae with some setae scattered over each tergite.

Ventral aspect a dirty white; coxae, in contrast to the legs, a whitish yellow outlined in dark brown; middle and anterior coxae with a subconical shape directed medially, the anterior coxae being more elongate in this direction than the middle ones. Abdominal sternites 1 to 7 membranous; normal in shape to the seventh; seventh sternite somewhat produced and bulged on its posterior margin; eighth sternite narrowed medially; ninth sternite produced on its posterior margin; tenth sternite much narrowed medially.

Mouthparts: Labrum twice as wide as long; anterior margin with fringe of short hairs progressively longer from the center outward. One mandible with three blunt teeth and a convex comb of short stout blunt spines below; the other mandible with six teeth and with a concave comb of short stout spines below. Each maxilla with lacinia terminating in a scoup bordered at the distal margin by four short blunt teeth and at the sides by rows of stiff hairs; galea conical, curved, and not as long as the lacinia; maxillary palpi long and stout. Labrum with glossae slightly longer than paraglossae and about half as wide; labial palpi very stout and short and not extending to the tips of the paraglossae; distal two segments of these palpi together almost egg-shaped.

DISCUSSION

This nymph runs to *Nemoura vallicularia* in Claassen's key to the known nymphs of *Nemoura*, from which it differs in the form of mouthparts as figured by Wu (1923: 57; figs. 14, 22, and 26) and pronotal markings as figured by Wu (1923: 53). This nymph of *Nemoura trispinosa* differs from the nymph of *Nemoura dimicki* (Frison 1936: 257) in the uneven distribution of setae on the hind femora and from the nymph of *Nemoura obscura* (Frison 1936: 259) by the presence of stout setae instead

Fig. 4. Nymph of *Nemoura trispinosa* (female).

Fig. 3. Nymph of *Taeniopteryx glacialis* (male).

of silky hairs on the hind femora and by the lack of a "tendency for a light longitudinal stripe on the abdominal tergites." From Seemann's key (1927: 53) to the stonefly nymphs of southern California, *Nemoura biloba* evidently has cervical gills since this is the key character used there for the genus. This nymph of *Nemoura trispinosa* differs from all other descriptions of American *Nemoura* nymphs in the presence of the four teeth of the lacinia and in the curvature of the combs of short stout spines on the mandibles.

A male of this species was taken at a bridge over a small stream midway between Frontenac, Minnesota, and the Mississippi River (a distance of about two miles) on May 30, 1939. The following season three nymphs of this species were taken at the same place, from which two females emerged and of which one was preserved in fluid. These females were *Nemoura trispinosa* as described and figured by Needham and Claassen. From the remaining female nymph the above description was made.

To the writer's knowledge this is the farthest west and also the earliest record for this species. Needham and Claassen recorded this species from Murray Bay, Province of Quebec, July or August, 1878, and from Tompkins Co., New York, June 17–20, 1904, and June 2, 1923. To these records can be added the following Minnesota records: 1 male, near Frontenac, Goodhue Co., May 30, 1939 (P. Harden); 3 nymphs (two of which were reared), Goodhue Co., May 25, 1940 (R. H. Daggy).

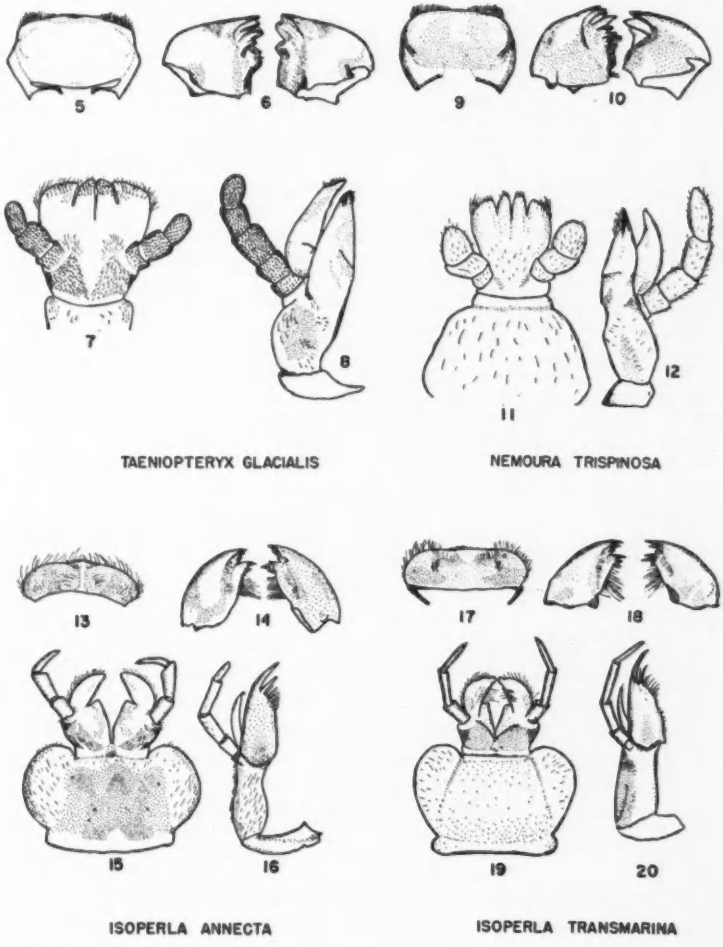
Isoperla annecta (Needham and Claassen)

(Figs. 1, 13, 14, 15, and 16)

1925 *Clioperla annecta* Needham and Claassen. Plecoptera of North America, p. 140–141.

Nymph.—General body color brown with yellowish white markings. Venter of thorax yellowish white with the venter of the abdomen becoming darker toward the posterior end. No gills present. Length of body of mature nymph 11 to 15 mm.; segments in antennae 50; segments in cerci 28.

Head with the brown areas anterior to the arms of the epicranial suture darker than those posterior to them. Light areas of the head are: a medium-sized area, squarish, heart-shaped or rounded, in front of the anterior ocellus; a much smaller spot, usually triangular, in the ocellar triangle; a large irregular spot from the inner margin of each compound eye extending medially to the nearest lateral ocellus; a small area on the posterior half of the stem of the epicranial suture; a light



Figs. 5–8. Mouth parts of the nymph of *Taeniopteryx glacialis*. Figs. 9–12. Mouthparts of the nymph of *Nemoura trispinosa*. Figs. 13–16. Mouthparts of the nymph of *Isoperla annecta*. Figs. 17–20. Mouthparts of the nymph of *Isoperla transmarina*.

stripe running inward and downward from the posterior margin of each compound eye. Antennae light at the base and darker toward the distal ends. The three ocelli form an approximate equilateral triangle, somewhat flattened; lateral ocelli slightly ahead of a line connecting the centers of the compound eyes, somewhat farther distant one from another than from one to a compound eye. Mouthparts as figured.

Pronotum oval, about twice as wide as long and with a marginal groove present along the anterior and the posterior margins; a dark line on the extreme lateral margins; a light area along each lateral margin; a median light stripe sometimes continuous and sometimes interrupted by dark spots; a light dot near the center of each half of the pronotum.

Mesonotum and metanotum with light markings; margins of wingpads light, leaving a wide brown central stripe down the center of each wingpad; another narrow short dark line near the lateral margin extending from the base partway out on each wingpad. Legs light with a darker band around the distal end of each femur and one around the proxal end of each tibia; sometimes a longitudinal dorsal dark stripe on the femur is more evident than the distal dark band.

Abdomen uniformly dark brown above; setae line the posterior margin of each segment. Cerci of about 28 segments; medium brown; distal segments many times longer than the proxal ones; a circle of setae on the posterior margin of each segment of the cerci.

The sexes of the nymphs may be distinguished. The female is larger, has a median notch in the posterior border of the eighth sternite, and has the setal fringe interrupted at this notch. The male nymph lacks this notch in the eighth sternite, has the setal fringe continuous at this point, and has the ninth sternite broadly produced behind.

DISCUSSION AND RECORDS

The Minnesota records for this species extend its range much farther west and place its time of emergence much earlier. Needham and Claassen give its records as Clinton Co., New York, June 21, 1910 (C. R. Crosby); and Quebec (Geo. Maheux). In Minnesota this species has been collected as early as April 5 and from that date through May in Hennepin County and in Anoka County, both near St. Paul. Rearings were made in 1935 by L. L. Smith and in 1940 by the writer.

This nymph runs to *Isoperla confusa* in Frison's key to the stonefly nymphs of Illinois (1935: 435) from which it differs in having a greater proportion of brown on its head, pronotum, and wing pads. It runs to *Clioperla similis* in Claassen's key to nymphs (1931: 69) from which it differs in being larger and in having a distinct color pattern on the head, pronotum, mesothorax, and metathorax.

Isoperla transmarina (Newman)

(Figs. 2, 17, 18, 19, 20)

1838 *Chloroperla transmarina* Newman, Ent. Mag., London 5: 499–500.
1839 *Chloroperla transmarina* Newman. Mag. Nat. Hist. N. S. 3: 87.
1908 *Isoperla ventralis* Banks. Psyche 15: 66.
1925 *Isoperla ventralis* Needham and Claassen. Plecoptera of North America, p. 150.
1938 *Isoperla transmarina* Ricker. Trans. Roy. Canad. Inst. 22: 146.

General color dull yellow with light brown markings which are predominantly longitudinal from the head to the extreme end of the abdomen. Length of body 10–12 mm.; segments in antennae 46; segments in cerci 25.

Head yellow with brown markings as follows: a triangle connecting the three ocelli and enclosing in the ocellar area a yellow triangle; areas from the sides of ocellar triangle extending outward to the bases of the antennae and forward to the distal margin of the clypeus, the anterior areas widening near the clypeus so that they become joined, thus enclosing an irregular yellow area in front of the anterior ocellus; a brown spot on each side of the stem of the epicranial suture; a line from the medio-caudal margin of each compound eye inward and downward to the margin of the foramen; a slight darkening toward the posterior margin of the head. Lateral tubercles shining dark brown. Ocellar triangle with the base slightly longer than the sides; lateral ocelli somewhat closer to the compound eyes than to each other and slightly ahead of a line connecting the midpoints of the compound eyes. Mouthparts as figured.

Pronotum over twice as wide as long; anterior and posterior margins nearly straight; lateral margins convex; all angles broadly rounded; marginal groove distinct across the median third of the anterior margin and across the posterior margin; posterior and anterior margins brown; longitudinal brown markings set off a median yellow stripe, and an elongate brown spot laterad of these set off a yellow lateral marginal stripe on each side; setal fringe present on the margin, the setae across the posterior margin being much longer than the others.

Mesonotum and metanotum predominantly yellow with brown longitudinal markings. Forewing pads with a narrow brown line running longitudinally, the line ending just inside the apex. Rearwing pads with longitudinal line forked near the apex.

Legs yellow with the usual row of long silky hairs on the outer margin. Tarsi not darker than the rest of the leg.

Abdomen with three dorsal brown stripes of about equal width running the total length, the median one being narrowed on the caudal segments. Tenth tergite with the posterior margin convex. Cerci with setae on the posterior margin of each segment; one ventral seta of this row on each segment much longer than the others.

DISCUSSION

This is another species listed by Claassen (1928) as one with type lost or inaccessible. Ricker (1938) recently described and figured the female type in the British Museum. The male

is that described as *Isoperla ventralis* by Banks (1908) and later by Needham and Claassen (1925).

In his description Banks (1908) described both male and female *Isoperla ventralis*. Needham and Claassen (1925) in their monograph of Plectoptera present figures and description of only the male. Banks replied, concerning a male and a female sent to him recently for comparison with types of *I. ventralis*, "Your male *Isoperla* agrees with the male except that yours is much larger. My specimens are dry, wing length but 8 mm. I cannot find the female I figured; there are three males, one made lectotype by Frison, in alcohol." Thus it is probable that Banks' original association of male and female was incorrect. This idea is supported by the fact that a male, agreeing with Needham and Claassen's description and figure, was taken May 19, 1940, in Chisago County, Minnesota, with a female agreeing with the male in shape and coloring, but being slightly larger. This female agrees with Ricker's redescription of *Isoperla transmarina*. In addition to the pair from Chisago County, spoken of above, several females from the same place were reared. The exuviae from these agree with a nymph taken at Fridley, Minnesota, May 6, 1931, this last nymph being the basis of the above description of this paper.

This nymph runs to *Isoperla bilineata* in Claassen's key to *Isoperla* in his "Plecoptera Nymphs of North America" and to the same species in Frison's key to *Isoperla* in his "Stoneflies or Plecoptera of Illinois." From this species *Isoperla transmarina* can be distinguished by its head pattern lacking the two large white spots on each side of the ocellar triangle, by its wing pad stripes being narrower, and by the abdominal stripes being darker and more sharply outlined.

It is evident that the nymphs of *Isoperla transmarina* inhabit medium to large rivers. The nymphs from Chisago County were taken from leaves and trash washed against a tree fallen into the North Branch River. The male and female were taken from a tree nearby.

DISTRIBUTION

This species has a northeastern distribution in North America. Newman's type specimen was, according to his original description (1838), from Trenton Falls, Canada, (possibly the region of Trenton Junction, Ontario). Banks' types of *Isoperla ventralis* are from Grand Lake, Newfoundland,

taken July 28, 1906. The Minnesota records include, besides those already mentioned from Chisago County, one female taken in Winona County, May 19, 1940.

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NEOPARACLETUS CARICIS, A NEW GENUS AND SPECIES OF APHIDAE (HOMOPTERA)

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Neoparacletus, new genus[1]

Antennae of six segments. Secondary sensoria in alate form numerous, small and oval. Absent in apterous form. Antennae with only a few short hairs. Apterous form with eyes composed of three facets; with occasional specimens having intermediate eyes. Cornicles absent. Cauda broadly conical, bearing numerous short hairs. Anal plate large, narrow, and bearing many short hairs. Each thoracic segment with a pair of well developed wax glands. Fore wings with the media simple; hind wings with both media and cubitus. Forms robust and live in close association with ants on the roots of *Carex*. Alatae rare. Sexuals unknown.

Genotype and only included species: *Neoparacletus caricis*, new species.

This genus is closely related to *Paracletus* by the number of segments in the antennae, the type of secondary sensoria, as well as in wing venation. It differs from *Paracletus* in the type of cauda and anal plate which in the later genus are rounded or luinar; while in *Neoparacletus* the cauda is elongated and approaches the elongated-conical caudae found in many species of the tribe *Aphidini*. The anal plate is elongated, narrow, with the tip rounded.

It also differs from *Paracletus* by having a pair of well developed wax glands on each thoracic segment, while *Paracletus* is in part characterized by having only a single centrally located wax gland on the mesothorax.

Neoparacletus caricis, n. sp.

Alate viviparous female.—Average length of body from vertex to anal plate 2.50 mm. Head black, pulverulent. Width of head through the compound eyes .50 mm. Eyes dark with ocular tubercles. Antennae of six segments: black in color. Length of antennal segments: II, .11 mm.; III, .40 mm.; IV, .20 mm.; V, .19 mm.; .14 mm., plus .03 mm. Sensoria on antennae distributed as follows: III, 53 to 65; IV, 22 to 26; V, 21 to 25; VI, 1 to 3. Rostrum obtuse, reaching slightly beyond third pair of coxae.

[1]The writer wishes to express his thanks to A. C. Maxson, of the Great Western Sugar Company, Longmont, Colorado, for his opinion concerning this form.

Thorax black, pulverulent. Prothorax yellowish. Each thoracic segment with a pair of well developed wax glands. Fore wings with the media simple. All veins failing to reach margin of wing. Hind wings with media and cubitous present. Legs black. Hind tibiae 1.10 mm.; tarsi .30 mm.

Abdomen sordid yellow, with conspicuous threads of wax along median line. First six segments of abdomen each with a pair of well developed wax glands. Cornicles absent. Cauda broadly conical, bearing numerous short hairs. Length of cauda .14 mm. Anal plate large, elongated and narrow, with the tip rounded and bearing numerous short hairs. The anal plate extends a little beyond the tip of the cauda.

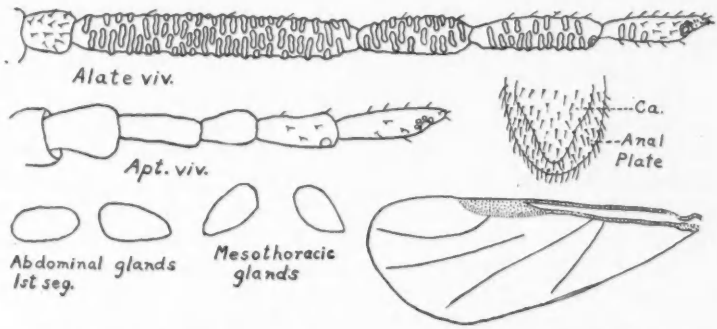

Fig. 1. *Neoparacletus caricis*, a new genus and species of Aphidae.

Apterous viviparous female.—Prevailing color milk white, with some individuals showing a tinge of light brown. Entire body covered with pulverulence. Length of body from vertex to tip of anal plate 2.90 to 3.80 mm. Head dusky. Eyes composed of three facets with some having intermediate eyes. Antennae composed of six segments. Early summer forms have antennae of only five segments. Antennae dusky in color. Length of antennal segments as follows: II, .11 mm.; III, .13 to .16 mm.; IV, .10 to .19 mm.; V, .13 to .15 mm.; VI, .15 to .17 mm., plus .03 mm. Secondary sensoria absent. Hairs on antennae sparse. Legs light brown to dusky in color. Rostrum obtuse and reaching well beyond the third pair of coxae. Cornicles absent. Cauda and anal plate dusky; in structure the same as alate. Length of cauda, .15 mm.

Host plant and feeding habits: This large new species was found feeding in large colonies on the roots of *Carex* sp. Alate viviparous females occur only in the fall, the summer generations being entirely apterous.

Type locality: Milwaukee, Wisconsin (National Home Grounds). *Holotype* alate viviparous female and *Morphotype* apterous viviparous female collected on Sept. 26, 1940. *Paratypes* collected on the following dates at same locality as types:

Aug. 22, 30, 31, 1939; June 25, July 6, 10, Aug. 13, 14, Sept. 26, 29, 1940 (Strom Coll.). Holotype deposited in the U. S. National Museum. Paratypes in the writer's collection and that of A. C. Maxson.

Toxoptera viridi-rubra Gill. and Pal.

This reddish brown species was collected by the writer in Wisconsin (Milwaukee Co.) on *Carex* on Nov. 4, 1936. Both apterous viviparous females and ovipara were found at this time. Two collections were also made by the writer at Grand Haven, Michigan, on June 8 and 12, 1936. This species has previously been recorded only from Colorado.

Thripsaphis verrucosa Gillette

Thripsaphis verrucosa Gill., Can. Ent., Vol. 49, p. 194, 1917.
Thripsaphis caricicola Swain, Ent. News, Vol. 29, p. 367, Dec., 1918, *New synonomy.*

This species has been recorded from California, Colorado and Illinois. It is easily recognized by having a peculiar projection from the vertex. In Wisconsin, the writer has collected it only in Milwaukee County, in a small *Carex* habitat at the National Home Grounds. However, whenever it is found it occurs in large numbers. All forms have been collected in Wisconsin.

The above synonymy is based on a study of cotypic slides of *Thripsaphis caricicola* Swain, kindly loaned to the writer by Dr. I. McCracken and specimens of *T. verrucosa* Gill. collected in Wisconsin. Hottes and Frison,[2] in their description of the apterous viviparous female of this species state that the antennae are without secondary sensoria. All specimens of this form examined by the writer show three small sensoria near the distal portion of antennal 111. These sensoria are very small and not readily seen. Cotypic specimens of *T. caricicola* from California and a large series of *T. verrucosa* collected in Wisconsin, all had two small sensoria near the distal end of antennal 111.

The male of this species is apterous and pinkish in color.

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[2]Hottes, F. C., and T. H. Frison, 1931. The Plant lice, or Aphiidae, of Illinois. Bull. Ill. State Nat. Hist. Survey, 19 (3): 121–447; 336 figs.

THE NESTING HABITS OF POLISTES WASPS AS A FACTOR IN TAXONOMY

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The suggestion is made by Dr. Robert Bugbee, in an interesting paper on *Polistes fuscatus* (Ann. Ent. Soc. Amer. 29: 614–616, 1936), that the nesting habits of *Polistes* wasps may be considered as another character for use in working out the phylogeny as well as the taxonomy of these wasps. He further states that a few clues in this line are now at hand, and more should be gathered since "the study of this aspect of behavior offers many interesting problems and angles." His remarks have still greater significance inasmuch as a study of the genus *Polistes* offers baffling difficulties to the taxonomist. Therefore any additional clues that their behavior can supply may in part answer the questions perplexing the taxonomist; or they may at least show the directions in which the various members of the genus are moving, psychologically.

In this region, four species of *Polistes* abound, of which only three, *P. pallipes*, *P. variatus* and *P. rubiginosus*, will be discussed in this paper. This is because these three species are given the status of varieties or color forms of the typical *P. fuscatus* by Dr. Joseph Bequaert in his important contribution on the Taxonomy of *Polistes* Wasps (Journ. N. Y. Ent. Soc. 48: 1–31, 1940).[1] The fourth local species which I have studied will not be discussed here because it is not so closely akin to the aforementioned three, and is placed in another category by Dr. Bequaert. These are only three of the eighteen which are designated as varieties or color forms of *P. fuscatus*. Apparently giving them this position was the only thing to do because specimens collected from a wide area show an intergradation of color, and also because of a lack of structural differences among the members of the *fuscatus* group. Dr. Bequaert almost despairs when he states that "North American Polistes are quite variable in the extent, arrangement and shade of color markings, and in *P. fuscatus* the color seems to run riot and defy any attempt at rational analysis."

[1]For the sake of consistency, I shall refer to them as species rather than varieties or color forms.

There are, however, two important features in our local *Polistes* fauna which help to overcome the difficulties which Dr. Bequaert has met. The first is the fact that, in spite of the intergradations of color in material from wide areas, our three species here are so distinct in color or pattern as to make them easily recognizable to the casual observer, even when the wasps are on the wing; ***rubiginosus*** is of a solid bright, brick-red color, ***variatus*** has yellow bands on a brown body, and ***pallipes*** has a somber black-brown body with slight traces of ferrugineous blotches. The second feature is that, even though there are insufficient structural differences to give specific rank to each one, there are psychological differences which culminate in distinctive patterns of nest-building and brood-care. These are the clues, as it were, which may indicate that they have traveled as offshoots from the parent stock and also the direction in which they are moving.

This brings us to the point of reviewing briefly the distinctive behavior patterns of these three species.

1. While all three species live in the same areas, each occupies a habitat of its own. *P. **pallipes*** builds its nests in well-lighted parts of man-made structures, under overhanging rocks and rarely in thickly matted vegetation. *P. **variatus*** nests in hollow places in the ground, under rocks on the ground where they may excavate a depression, in tin cans or old pans on rubbish dumps. *P. **rubiginosus*** always nests in dark places, in hollow trees or in the space between the outer and inner walls of old buildings (Bull. Brook. Ent. Soc. 26: 111–118, 1931, and Ecology 10: 191–200, 1929).

2. There is murderous antagonism between the species; each one has traveled so far in its own divergent way from the parent stock that they even recognize one another as enemies (Journ. Comp. Psychol. 10: 267–286, 1930, and 27: 259–269, 1939). Dr. Bequaert suggests that one possible way to solve the species problem in *Polistes* is by a study of the heredity in color pattern by crossing them, but this antagonistic attitude precludes that. In nature also, crossing is not likely to occur for the additional reason that, even though they live in the same area, each occupies a different niche in it and they do not mingle. At least I am sure of this for *P. **rubiginosus***, in which species mating occurs near the nest (Ent. News 40: 7–13, 1929).

3. Pleometrosis occurs in *P. **rubiginosus***, nests being founded by few or many queens, sometimes as many as seventeen (Psyche 38: 129–144, 1931), while in *P. **pallipes*** and *P. **variatus*** each nest is founded by but one queen (l c., footnote, p. 134. Additional data in course of publication).

4. Even though nests of ***pallipes*** and ***variatus*** are founded by single queens and begun at the same time of the year, the nests of ***variatus*** are much larger than those of ***pallipes*** before the end of summer (paper in course of publication).

5. When the places of hibernation of the three species are considered, some differences are found. *P. **rubiginosis*** has been found hibernating only in hollow logs, while ***pallipes*** and ***variatus*** have been found sheltered for the winter behind closed shutters or other nooks about buildings.

6. *P. rubiginosus* which build in close, dark places, is the only one of the three which has guards at the knot-hole entrance to the nest, and I have actually seen them keep out intruders. But the primary purpose of these doormen is to ventilate the nest in its close quarters. The others, which build in light, airy places, do not need this type of specialization, and they do not have it.

7. Under normal conditions, all three species make round nests with the pedicel in the center. These they attach to horizontal surfaces, hence the nests also hang in a horizontal position. However, *P. pallipes* sometimes attempts to hang a nest horizontally on a vertical wall instead of on the adjacent ceiling. When this is done, the nest seldom attains full size, and is often abandoned early in its development. One sometimes sees numerous dabs of paper-pulp plastered on a vertical wall where a stupid queen has made many attempts at building a pedicel but finally gave up the project. The item of interest in this connection is that when this condition occurs one usually finds several such nests in one place as though they had been produced by a certain "strain" living in that area. My point in citing this behavior is to show that certain *pallipes* have broken away from the customary habit of their own kind and are doing this one thing differently. The wisdom of this digression need not be discussed here; it suffices to say that it was needless, since ample ceiling space was near by. However, this trait seems to have become fixed to some degree in their heredity, for whenever I find this condition in a barn or a shed, I usually find similarly distorted nests from previous years nearby. It is true that certain *Polistes* wasps in the tropics place their nests on vertical walls, but they build the pedicel at the top and let the nest hang vertically in a pear-like form.

The behavior patterns enumerated above would give *pallipes*, *variatus* and *rubiginosus* the status of physiological races, according to taxonomists. Bequaert himself recognizes this status, for he says (l. c. p. 6) that "perhaps we are dealing here with ecological, physiological or even behavioristic races." It seems, therefore, that the conditions which we view in the above three categories are somewhat midway between the lower categories of Bequaert and the status of full-fledged species, and that these distinct behavorial adaptations bring them well on the road to becoming true species.[2] Today, it is true, they offer nothing tangible for the taxonomist to work upon, but this is evidently due to the fact that structural modifications have not yet caught up with the psychical advances which are driving the offshoots of a simple parent stock in three directions. Persistence in these separate directions and the mutual antagonisms will doubtless eventually intensify the differences already evident. That psychical changes should occur under our eyes today is no more strange than that they have occurred in ages

[2]It seems that this study fulfills the prediction of Dr. A. E. Emerson, who says in a recent review of Huxley's book, "The New Systematics," "Inasmuch as the species is a stage in the evolutionary process, we should expect to find stages leading up to the species in some instances. Such discoveries help in understanding the essential processes of speciation, and help to clarify the dymanic nature of the species."

past. At one time, members of the genus *Polistes* were few and of simple habit. Diversification has brought them to the various states we see today. But all this merely points to the probability that organisms have first to change some essential item in their mode of living before a structural modification can gain a foothold. We have in these three groups evidence that the physical form remains stable while the mental activities change; behavior is much more plastic than structure, and in the race of evolution behavior may be, chronologically speaking, miles ahead of morphological change. This is held to be true, not so much by the laboratory student as by persons who spend much time in the field. The late Dr. W. M. Wheeler was one who studied insects in their native surroundings. I quote a paragraph from his "On Instincts" (Essays in Philosophical Biology, p. 49, 1939):

"I can only state * * * my conviction that structure is after all the visible, highly mechanized end-stage of function, and that our inability to detect the inheritance of an acquired character is probably due to the fact that its visible appearance is preceded in phylogeny by a period of many generations during which it is inherited only as a function associated with alterations of structure too subtle to be revealed by our present very crude methods of observations and experiment. Inheritance of alternative characters in definite Mendelian ratios would therefore be merely the method of inheritance of stereotyped end-products of a long evolution and would not represent the actual phylogenetic method of development of such characters."

INSECTOS DO BRASIL, 3.° TOMO, HOMÓPTEROS, by A. DA COSTA LIMA, pp. 1-327, 267 figs., 1942. Published by the Escola Nacional de Agronomia in its Série Didática, N. 4.

This excellent volume is the fourth of the general work, Insectos do Brasil, being published by Prof. A. da Costa Lima, Professor of Entomology in the National School of Agriculture. When completed this work will be the first general work on tropical entomology in the Portuguese language that can be used in the higher schools of Brazil. Prof. Costa Lima has written many articles on tropical Homoptera, particularly on scale insects, so that volume 4 is in his own field of scientific work.

In the more than three hundred pages of text no attempt has been made to give lists or keys to species or even to genera. The author has had to choose material carefully and has given us a volume that brings together what is known on structure, life history and economic relations of the Homoptera. Even in his own group, the Coccoidea, keys run only to subfamilies and to tribes. The illustrations are numerous (267 figures) and well done. We see the artists signatures, C. Lacerda, Jm. F. Toledo and De Costa Lima. The press work is good and the quality of paper of the best. We regret the lack of space in the Annals for a more detailed outline of this work.—C. H. K.

SOME OBSERVATIONS ON REARING ODONATA IN THE LABORATORY

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The difficulties of rearing Odonata under laboratory conditions have long prevented the use of a desirable type of material in both teaching and research. Some half dozen other insect orders have attained important places in research largely because of the comparative ease with which they could be bred and reared under experimental conditions. Morphology, embryology, physiology, and genetics have profited enormously.

Almost untouched, however, are certain fundamental conditions which are prominent in the Hemimetabola, and especially in such insects as involve both aquatic and terrestrial environments in a single life cycle. Of these orders the Odonata is outstanding. The late Dr. R. J. Tillyard wrote his "Biology of Dragonflies" (8) in the expressed hope, unfortunately not realized, that it might stimulate an interest in bringing odonate materials into more general use. Undoubtedly the obstacles in the way of using the Odonata are greater, though not insurmountable, than in many other groups, but the problems afforded by their study are attractive and fundamental. Awaiting attack are further investigations on growth, involving both morphology and physiology; the course and causes of transformation; the presence and activities of endocrines as yet unknown; the cytology of metamorphosing tissue cells as well as that of germ cells; and the accurate determination of many life histories. Granted that some of these problems have been investigated in the Metabola it is still true that they may be seen more clearly and perhaps from a better phylogenetic viewpoint in the less complex forms.

It is these facts that have prompted the writer to add some of his own experiences in rearing Odonata to the records available, mainly those of Needham, Calvert (1), (2), (3), Grieve, and a few others. All but one of these has been concerned chiefly with larval stages and have little to say of rearing adults in captivity.

The aquatic environment of the larva and the terrestrial requirements upon the adult are so far separated that rearing techniques must follow distinct methods.

REARING LARVAE

The rearing of nymphs in their natural habitats during summer has been extensively covered by Professor Needham (5), (6), (7), and others. When the work is done in the laboratory and is carried throughout the year modified aquarium methods must be used. In addition to green plants for chemical balance and mechanical support, isolation of the individuals must be effected by screens, separate aquaria or finger bowls to prevent constant losses through cannibalism.

While the problem of feeding larvae is not a difficult one the writer has found certain variations an advantage in the cases of such Anisoptera as *Anax*, *Aeshna*, *Tramea*, *Sympetrum*, etc. Bits of frog's liver or other soft tissue (mature vertebrate muscle and connective tissue seem either too tough or too concentrated) may be substituted for the usual mealworms or insect larvae carried in cultures as a food supply. Such food is always at hand in any laboratory and seems well adapted to the nourishment and growth of nymphs of medium and large size at least. From 1937 to 1940 numbers of specimens varying from a dozen to over fifty at a time have been thus experimentally fed and carried along. Two or three feedings a week were given. The larvae, when not parasitized, always ate voraciously, and molted at apparently normal intervals for the season. In order to insure the proper amount of food and to prevent the fouling of the aquaria most of the feeding was done by hand. A bit of liver was held in forceps before the larva and if the latter did not respond promptly it was picked up between thumb and finger, when defensive thrusts of the labium resulted in the seizure of the food. The insect was replaced in the water where it continued to rapidly ingest.

This method has the advantages of certainty respecting the kind of food taken, the amount ingested at one feeding, and the number of feedings necessary under varying conditions. Further, it makes possible, in specimens with semi-transparent bodies, investigation of the progress of food down the alimentary canal and of digestion in each of its divisions. This is particularly true in freshly molted specimens and in such genera as *Tramea*. These individuals gorge themselves rapidly, filling the crop quickly, while the passage of the food to the ventriculus and intestine proceeds gradually over a period of many hours or even two to three days. Such observations have been made by the writer on several genera and in various stages. Opportunity is here given, also, for studying such fairly constant movements of portions of the digestive tract as peristalsis and the oscillation of the ampulla.

Observations of especial interest may be made during the period immediately preceding emergence, the reorganization of the labial muscles gradually making feeding impossible, and allowing for the complete emptying of the alimentary canal.

REARING ADULTS

The aerial habit and extreme activity of adult Odonata usually make captivity fatal. Miss Grieve's account of the rearing of *Ischnura verticalis* (4) is the only one known to the writer. As this species is one of the smaller damselflies the problem of captivity in fairly normal habitat conditions can be met by the use of sizable aquaria covered by screened enclosures and supporting adequate vegetation. While such a method might possibly be adapted to smaller Libellulids, no records are known. The Aeshnids, however, are large, swift of flight, and long of range. Further they are voracious feeders and have never been known to capture living prey placed in their cages. Their adult period is, also, weeks in length. Thus the methods used with the smaller weaker fliers are not applicable.

The age of specimens taken in the field cannot be determined with accuracy, and if studies are to be made upon the development of glands and their physiological relations to reproduction, longevity and other functional conditions, individuals must be reared from emergence to reproductive maturity at least and possibly to normal death.

To attain these results the writer has collected large numbers of nymphs during the summer and carried them through to emergence. Each morning the tenerals which have emerged during the night, normally between eleven P. M. and two A. M., are placed in individual glass battery or other jars of similar size and covered with wire screens of coarse mesh (¼″). These cages are placed in a north window with plenty of fresh air. Here the dragonflies hang without attempt at flight as the distended body hardens. In forms like *Anax* and *Aeshna* no food is taken for at least two days due to the gas-inflated gut. The period is shorter in smaller species.

On the third day each Aeshnid individual is offered soft living or fresh food passed through the screen on the tips of forceps, but no effort is made to force the insect to eat. Very soft-bodied flies or jelly-like muscles scraped from the bodies of large nymphs are used. As the days pass larger and heavier flies, etc., are given, and in case the captive refuses to accept the food readily it is held by the wings and the food introduced into its mouth as it bites at its captor. Once the food juices are tasted mastication continues and the insect may again be hung from the wire roof of its cage. But one feeding a day is given at first but with increasing age the number is increased to two or three, each being equivalent to one or two medium sized flies.

The motions of the mouth parts are of interest. When closely observed under a Greenough binocular microscope equipped with 32 mm. objectives the actions of individual parts may be followed. The labium provides a basket or trough within which the food is rotated (1) by the alternating grasping actions of the mandibles and the maxillae, (2) by slight forward thrusts of the labium, and (3) by the rotating manipulations of the bristle-covered hypopharynx. The spines on the lateral divisions of the labium, together with the finer bristles along the labial margins, prevent the masticated food from escaping. Thus the shearing action of the mandibles and maxillae reduce the fly or other

prey to a soft pulpy ball which decreases steadily in size as it rotates, and until the last small remnant is swallowed.

By this method of hand feeding, adults have been kept alive and apparently normal for more than a month. One specimen's food consumption was carefully recorded by the writer. In twenty-eight days it ate some seventy flies (*Musca*, etc.) in addition to the scraped muscles of a dozen large Anax nymphs. Its excreta, after drying in a vial for some weeks, weighed .207 grams.

There was, however, considerable variation in the survival ages of different specimens. Some lived but a day or two; many died at about fifteen to sixteen days, those surviving beyond this amounting to about 30 per cent. At times death was due to neglect of proper feeding, but at others the causes were not clear. Over-feeding or the eating of too much heavy chitin often seemed the cause. In the latter case dissection exposed masses of chitin clogging the entrance to the ventriculus, and it was this discovery which led to the feeding of muscle scrapings from nymphs or of other pulpy food during the first few days after emergence, and at all times to the avoidance of insects having heavy skeletons. The type of food also played a part. *Anax* and *Aeshna* refused such flies as *Callifera* and *Lucilia*, while eating *Musca* greedily

Temperature conditions seem important; many deaths occurred on hot days, especially if plenty of fresh air was not provided. At such times, also, some individuals became so active as to beat themselves to death.

While the death rate seemed markedly affected by the conditions just mentioned, there were, also, differences produced by more fundamental nutritional and physiological conditions; some died within a few days while others survived for several weeks. Probably some were parasitized, but it would seem possible that the nutritional conditions affecting the life of the last instar might be carried over into the imago, determining its physiological state and causing variation in physical stamina.

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ON THE STOMODAEAL NERVOUS SYSTEM OF INSECTS[1]

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The term, stomodaeal nervous system, is used by Snodgrass (1935) as the name for the system centering in the stomodaeal ganglia and having nerve fibers extending to the stomodaeal part of the alimentary tract. During the last hundred years, several different names have been applied, principally sympathetic, visceral, pharyngeal, and stomatogastric. Although the last word is widely used today, it is not sufficiently inclusive since various parts of the stomodaeum such as the salivary glands and aorta are innervated by fibers extending from the ganglionic centers of the stomodaeal nervous system. In addition the alimentary tract is innervated by a system of nerves emanating from the posterior abdominal ganglion of the ventral nerve chain. Furthermore the term, stomodaeal, first proposed by Janet (1899), seems especially fitting for this system of nerves and ganglia because the ganglionic centers arise during embryonic development by ingrowths from the dorsal wall of the stomodaeum.

Müller (1828) first offered the analogy with the sympathetic nervous system of vertebrates which is still retained in a modified form. The vertebrate sympathetic nervous system is a part of the autonomic nervous system which innervates various glands, the heart and blood vessels, and certain viscera as does the stomodaeal nervous system in insects. Here the analogy ends, however, for regulation of the breathing mechanism of vertebrates is an important function of the autonomic nervous system; while in insects the spiracles and tracheae receive nerve fibers directly from the ventral nerve cord. The vertebrate heart is innervated exclusively by fibers from the autonomic nervous system, but nervous control of the hexapod aorta is maintained through connections from both the stomodaeal system and the ventral nerve cord.

[1]The subject matter of this paper formed part of a thesis submitted to the faculty of the Graduate School of the University of Maryland in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Grateful acknowledgment is made of the help of Mr. Robert E. Snodgrass, who directed the work, and Dr. Ernest N. Cory, Head, Department of Entomology.

The variation in number and position of the nerves and ganglia of the stomodaeal nervous system makes it somewhat useless to describe any typical arrangement although there are a few fairly constant features such as the frontal ganglion and the recurrent nerve. Further generalization is complicated by the terminology which has become more confusing with each addition to the literature. Existent information with one or two exceptions has been published incidentally along with studies of the central nervous system, corpora allata, histology of the brain, and embryology. In this connection the papers of Blanchard (1858), Janet (1899), de Sinéty (1899), Bordas (1900), Holste (1910), Nabert (1913), and de Lerma (1933, 1937) should be mentioned as the most outstanding.[2] Recent interest in the subject of insect endocrinology has been intensified by much experimental work but has been accompanied by a sort of lag in morphological investigations.

THE STOMODAEAL NERVOUS SYSTEM OF A GRASSHOPPER

In the literature are found descriptions of the stomodaeal nervous system of several members of the order Orthoptera. In the present paper the stomodaeal nervous system of the grasshopper, *Schistocerca americana* (Drury) is described not because it is necessarily typical of this order but because it can be adapted to a clarification of the nomenclature and because it will serve as a starting point for an explanation of the numerous differences in arrangement which exist.

In *Schistocerca* (fig. 1) the frontal ganglion (Fr Gng) lies just above the pharynx in front of and slightly below the brain with which it is connected by the frontal ganglion connectives (Fr Gng Con). These bilateral connectives were called the arched nerves in the early literature. The recurrent nerve (R Nv), which has been termed the sympathetic, stomatogastric, and gastric nerve, extends posteriorly from the frontal ganglion, and following the dorsal wall of the pharynx and oesophagus runs under the brain and into the occipital ganglion slightly caudad of the brain. The occipital ganglion (Oc Gng) has been named the hypocerebral, the pharyngeal, the oesophageal, the subcerebral, and the anterior visceral ganglion by various authors. The word, occipital, should be restricted to the median ganglion which is penetrated anteriorly by the fibers of the recurrent nerve and which in *Schistocerca* and many other insects appears as a swelling of the recurrent nerve.

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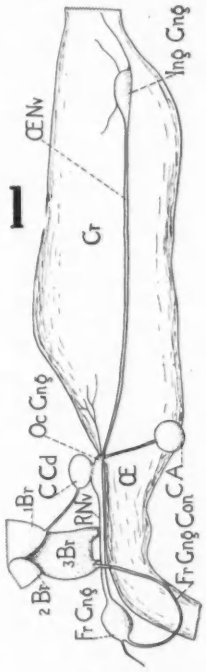
[2]Since this paper was submitted for publication, two related papers have become available and should be added to this list. They are:

Hanström, B. 1940. Inkretorische Organe, Sinnesorgane und Nervensystem des Kopfes einiger niederer Insektenordnungen. Kungl. Sv. Vetenskapsakad. Handl. (3rd Series) Bd. 18, no. 8: 1–265, figs. 1–239.

Nesbitt, H. H. J. 1941. A comparative morphological study of the nervous system of the Orthoptera and related orders. Ann. Ent. Soc. Amer. 34: 51–81, pls. 1–7.

Branching dorsally from the occipital ganglion are the paired corpora cardiaca (C Cd) each of which is joined to the brain by a short nerve. These structures have been called the anterior oesophageal or pharyngeal ganglia. They are called pharyngeal bodies by de Lerma



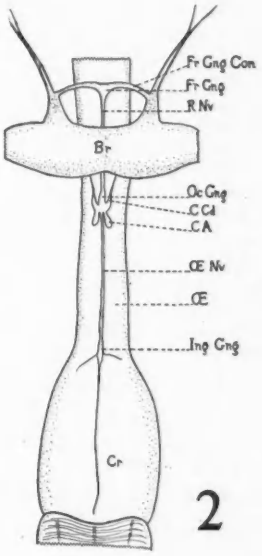


Fig. 1. Lateral view of Stomodaeal Nervous System of *Schistocerca americana* (Drury).

Fig. 2. Dorsal view of Stomodaeal Nervous System of a Dragonfly Naiad (unidentified); aorta removed.

EXPLANATION OF THE ABBREVIATIONS USED:

Ao—aorta
Ant—antennal
Br—brain
1Br—protocerebrum
2Br—deutocerebrum
3Br—tritocerebrum
CA—corpus allatum
CCd—corpus cardiacum
Coe—circumoesophageal
Con—connective
Cr—crop
Fr—frontal
Gng—ganglion
Ing—ingluvial
Lm—labral
M—muscle
Nv—nerve
Oc—occipital
OE—oesophagus, oesophageal
Op—optic
Phy—pharynx, pharyngeal
Pmp—pump
R—recurrent
Soe—suboesophageal
Vent—ventriculus

(1933, 1937) who has presented histological evidence of their glandular nature in the oriental cockroach and other insects. The term corpora cardiaca was originated by Pflugfelder (1937A) whose studies on the phasmid, *Dixippus*, have not yet furnished experimental proof of the secretory nature of these bodies. Pfeiffer (1939) suggests the possibility that a hormone secreted by the corpora cardiaca may be associated with the molting mechanism in the grasshopper, *Melanoplus*.

In *Schistocerca* the paired corpora allata (C A) are located below and slightly posterior to the occipital ganglion with which they are connected by short nerves. Extensive histological, embryological, and experimental investigations have established the fact that the corpora allata are glands of internal secretion, but a discussion of this work is outside the scope of this paper. Suffice it to say that hormones secreted by the corpora allata probably have different functions in different species of insects; that there is no positive proof that the corpora allata are the source of the hormone which influences molting; that there is experimental evidence to show that in some insects a hormone secreted by the corpora allata controls metamorphosis; and that by removal of the corpora allata from certain hemimetabolous insects it has been demonstrated that they are the source of a hormone necessary for normal reproduction.

Extending posteriorly from the occipital ganglion in *Schistocerca* there are two pairs of nerves. One pair soon branches along the dorsolateral oesophageal wall and the anterior wall of the crop and sends fibers to the aorta. The other pair of nerves, the oesophageal nerves (OE Nv), run along the lateral walls of the oesophagus and crop. In many insects there is a single oesophageal nerve, and whether paired or unpaired the same nerve has been called the pharyngeal, the ventricular, the gastric, the stomatogastric, the vagus, and the sympathetic nerve, and it has been referred to as a paired or unpaired continuation of the recurrent nerve. The word oesophageal seems more appropriate than any of the other names because the nerve, whether paired or unpaired, runs for most of its course along the oesophagus, and many small branches innervate the oesophageal wall.

EXPLANATION OF FIGURES IN PLATE I

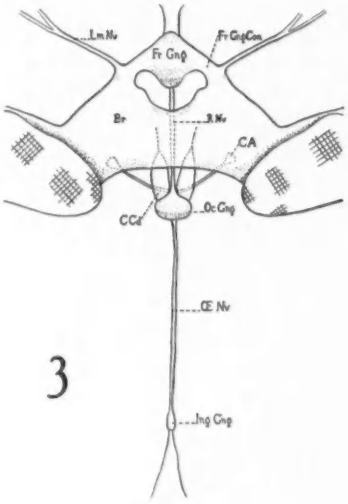
Fig. 3. Dorsal view of Stomodaeal Nervous System of *Libellula* sp. (adult); aorta and oesophagus removed.

Fig. 4. The Stomodaeal Nervous Stysem of *Magicicada septendecim* L.
A. Lateral view; M, dilator muscle, attachment to pharynx not shown.
B. Frontal view of corpora cardiaca and corpora allata, somewhat diagrammatic.
C. Posterior view of corpora cardiaca and corpora allata; aorta and oesophagus not shown.

Fig. 5. The Stomodaeal Nervous System of *Nezara hilaris* Say.
A. Dorsal view; aorta partly removed.
B. Dorsal view, detail of postcerebral structures; aorta and oesophagus removed.
C. Ventral view; oesophagus removed.

Fig. 6. Dorsal view of Stomodaeal Nervous System of *Arilus cristatus* L.

(See page 345 for explanation of abbreviations.)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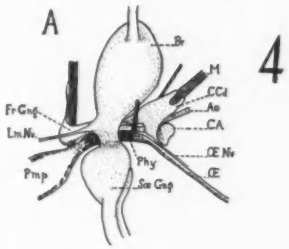
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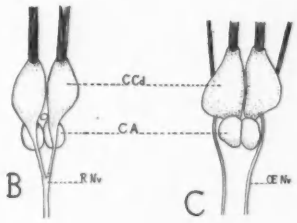
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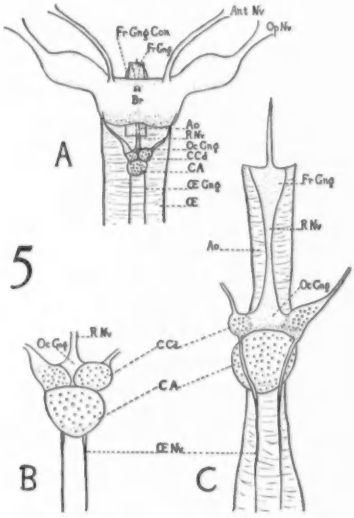
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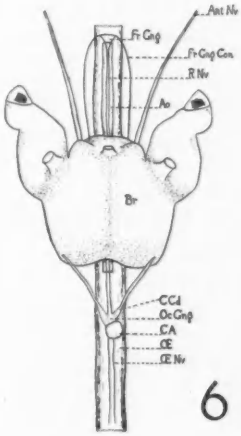
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The oesophageal nerves end in the ingluvial ganglia which have also been called the vagus, the splanchnic, the visceral, and the stomachic ganglia. In some insects there is a single ingluvial ganglion; in others it is absent. The ingluvial ganglia in *Schistocerca* are well developed. They lie along the posterior lateral walls of the crop which are innervated by several branches from them.

THE STOMODAEAL NERVOUS SYSTEM OF A DRAGON FLY

In a dragonfly naiad (fig. 2) the frontal ganglion connectives arise from tritocerebral lobes of the brain which extend anteriorly to the labrum. The recurrent nerve runs back under the brain on the dorsal wall of the pharynx to the occipital ganglion. From this ganglion the corpora cardiaca branch anteriorly and the corpora allata, posteriorly. These five structures are very closely associated with each other. A short nerve connects each corpus cardiacum with the protocerebrum. A single oesophageal nerve runs posteriorly to the ingluvial ganglion which lies on the dorsal wall of the oesophagus where the latter begins to enlarge and form the crop. The corpora cardiaca are slightly dorsad of the occipital ganglion, and the aorta runs between them and stops just behind the brain.

In the adult dragonfly (fig. 3) the frontal ganglion is close to the brain and the frontal ganglion connectives are short and thick. In contrast to their position in the naiad, the corpora cardiaca are slightly ventrad of the larger part of the occipital ganglion, and the anterior parts of them are situated under the brain with which they are connected by short, thin nerves. The corpora allata also are located under the brain. They are much farther from the occipital ganglion in the adult than in the naiad. The median oesophageal nerve connects the occipital ganglion with the ingluvial ganglion which is located on the dorsal wall of the anterior part of the crop. A pair of nerves extends posteriorly from the ingluvial ganglion.

Microtome sections[3] of the corpora cardiaca and occipital ganglia of several dragonfly adults gave no indication of the glandular nature of those structures. They appear to consist of nervous tissue, but sections of the corpora allata showed that these bodies were composed of vacuolated cells of a glandular type.

[3]The insects were fixed in toto in Carnoy—Lebrun and Bouin's fluids, either of which gave good results. The parts to be sectioned were dissected out before embedding. Standard haematoxylin was a satisfactory stain.

EXPLANATION OF FIGURES IN PLATE II

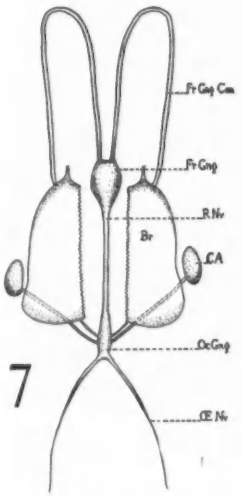
Fig. 7. Dorsal view of Stomodaeal Nervous System of the Larva of *Passalus cornutus* Fab.

Fig. 8. Dorsal View of Stomodaeal Nervous System of *Prodenia eridania* Cram. Adult.

Fig. 9. The Stomodaeal Nervous System of *Sceliphron cementarium* (Drury). A. Dorsal view. B. Lateral view.

Fig. 10. The Stomodaeal Nervous System of *Erax* sp. A. Lateral view. B. Frontal view.

(See page 345 for explanation of abbreviations.)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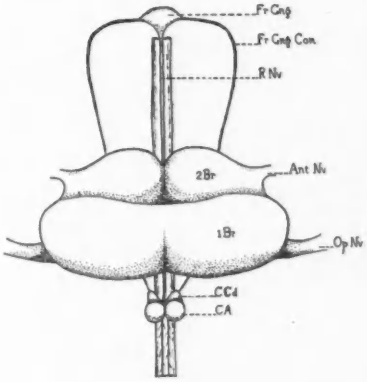
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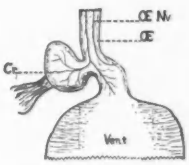
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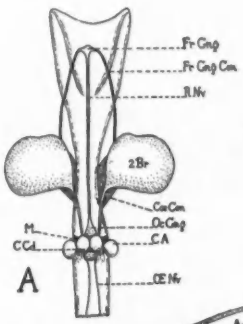
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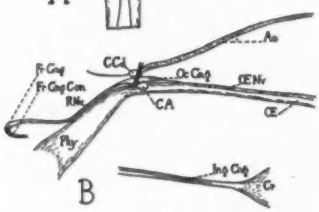
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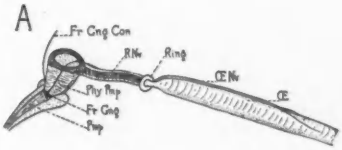
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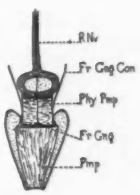
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THE STOMODAEAL NERVOUS SYSTEM OF A CICADA

In *Magicicada septendecim* L. (fig. 4) the frontal ganglion is located just above the stomodaeum near the junction of the latter with the sucking pump. The short recurrent nerve runs under the brain, then bifurcates. The branches run to the paired corpora cardiaca which are irregular in shape and practically surround two of the dilator muscles of the pharynx. (The attachment of this pair of muscles to the pharynx is omitted in fig. 4A). Paired oesophageal nerves pass posteriorly from the corpora cardiaca, but there are no ingluvial ganglia. The paired corpora allata are in contact with the posterior ventral parts of the corpora cardiaca. All of these bodies are dorsad of the stomodaeum. Nerves passing from the corpora cardiaca directly to the brain were not found.

With regard to the absence of a distinct occipital ganglion in the cicada, it is of interest to note that according to Bugnion (1908) such a structure is not present in the lantern-fly, *Fulgora*, and that Pflugfelder (1937B) found no occipital ganglion but distinct corpora cardiaca in the aphid, *Pemphigus*. However, according to the same author the scale insect, *Lecanium*, appears to have a distinct occipital (hypocerebral) ganglion but lacks corpora cardiaca.

THE STOMODAEAL NERVOUS SYSTEM OF A BUG

In the green stink bug, *Nezara*, (fig. 5) the frontal ganglion is a triangular structure, somewhat flattened. The recurrent nerve is short and rather large in porportion to the other nerves. The corpora cardiaca are fused ventrally but are distinctly lobed dorsally. They form a plexus with the occipital ganglion from which the paired oesophageal nerves originate. The latter pass under the unpaired corpus allatum which is contiguous with the posterior part of the plexus mentioned above.

In the wheel bug, *Arilus* (fig. 6) the recurrent nerve is longer than in *Nezara*. The postcerebral parts of the stomodaeal nervous system are similar to those of *Nezara*. There is a fusion of the corpora cardiaca with the occipital ganglion, and the corpus allatum rests on the posterior part of this mass. Numerous specimens of these two bugs were examined, and it was found that the asymmetry of the corpora cardiaca and corpus allatum is rather constant—a condition which has been observed in other orders of insects.

THE STOMODAEAL NERVOUS SYSTEM OF A BEETLE

The general pattern of stomodaeal innervation was found to be similar in the green June beetle, *Cotinis nitida* L., and in the larva of *Passalus cornutus* Fab. The frontal ganglion connectives in the larva of *Passalus* (fig. 7) run forward a considerable distance before turning back to the tritocerebrum. Corpora cardiaca were not observed; it is possible that they are fused with the occipital ganglion, for there is a pair of nerves joining it to the brain. The paired corpora allata are located at the side of the brain and the nerves which join them to the occipital ganglion run under the brain. From the occipital ganglion the

paired oesophageal nerves branch posteriorly and follow the oesophageal wall. Ingluvial ganglia are absent.

THE STOMODAEAL NERVOUS SYSTEM OF A MOTH

The stomodaeal nervous system of lepidopterous larvae has been reported to be rather complex. In the larva of *Protoparce sexta* Johanssen the pattern of stomodaeal innervation appears to be similar to that of a noctuid caterpillar described by Snodgrass (1935). The paired corpora cardiaca (lateral anterior ganglia) are some distance from the recurrent nerve, and there is no distinct occipital ganglion. From each corpus cardiacum, in addition to the nerve joining the recurrent nerve, there are fibers passing to the brain, the mandibular nerve, the mandibular muscles, and the corpora allata. Nerves from each corpus allatum run to the corresponding salivary duct. It is probable that there is a sheath of nervous tissue surrounding the corpora cardiaca and allata. A small ingluvial ganglion is present.

The stomodaeal nervous system of the southern army worm moth, *Prodenia eridania* Cram. (fig. 8) is quite different from that of lepidopterous larvae. The corpora cardiaca are fused and the median parts of them are joined by the recurrent nerve to form what is probably the occipital ganglion. Two oesophageal nerves extend posteriorly from this mass, part of which is between the ventral parts of the corpora allata. The dorsal parts of the corpora allata are in contact with each other. About halfway down the oesophagus each of the oesophageal nerves sends off a lateral nerve to the salivary glands. Many short nerves branch from the oesophageal nerves to innervate the oesophagus; and the crop, which is a lateral diverticulum, is innervated by branches from them. They end in numerous fine fibers anterior to the ventriculus.

THE STOMODAEAL NERVOUS SYSTEM OF A WASP

In the wasp, *Sceliphron cementarium* (Drury) (fig. 9) the frontal ganglion is rather small and the recurrent nerve runs posteriorly from it to a distinct occipital ganglion. The corpora cardiaca are located above the latter and are connected with the deutocerebrum by rather thick nerve fibers. Below the occipital ganglion on each side of it are the corpora allata. Paired oesophageal nerves pass from the occipital ganglion to the two small ingluvial ganglia on the sides of the narrow posterior part of the oesophagus.

THE STOMODAEAL NERVOUS SYSTEM OF A ROBBER FLY

In connection with experimental work on the cause of pupation in various Diptera, Burtt (1937) studied the stomodaeal nervous system and found that in *Chironomus* and *Tipula* larvae there are well-defined occipital ganglia, corpora cardiaca (oesophageal ganglia) and corpora allata. An investigation of the larva of *Tipula abdominalis* Say has essentially corroborated the description given by Burtt.

Many of the early investigators described a ring of supposedly nervous tissue surrounding the aorta behind the brain in cyclorrhaphous Diptera. Recent experimental work by Hadorn (1937), Burtt (1937A,

1937B) and De Bach (1939) has indicated that this group of cells known as Weismann's ring secretes a hormone inducing pupation in *Drosophila*, *Calliphora*, and *Musca*. Fraenkel (1935) states that there exists in *Calliphora* larvae no organ which can be homologized with the corpora allata in other insects.

It is of interest to note that Weismann's ring has so far been reported to exist only in cyclorraphous Diptera. In the robber fly, *Erax*, a similar ring is present. In this insect (fig. 10) the frontal ganglion rests on the anterior wall of a pharyngeal or secondary sucking pump. Dorsally and posteriorly the pharynx has a circular sclerotic plate with a narrow extension to the beginning of the oesophagus. Large muscles are attached to the circular plate, and the recurrent nerve, following the dorsal wall of the pharynx, wends its way between the muscles. Along the extension of the plate the recurrent nerve swells to form what is possibly an occipital ganglion. At the union of the pharynx and oesophagus, the ring of tissue mentioned above surrounds the gut. The recurrent nerve unites with this ring. Posteriorly an oesophageal nerve leaves the ring and passes along the dorsal wall of the oesophagus. Near the end of the oesophagus the nerve bifurcates, but there are no ingluvial ganglia. The frontal ganglion connectives are apparently the only nerves extending from the brain to the stomodaeal system. Whether the ring described above corresponds to the corpora cardiaca or corpora allata is unknown. However it seems logical that it is the homologue of Weismann's Ring.

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KEY TO THE NEARCTIC GENERA OF WATER BEETLES OF THE TRIBE AGABINI, WITH SOME GENERIC SYNONYMY

(Coleoptera: Dytiscidae)[1]

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Upon using the key to the genera of the tribe Agabini as given in Bradley's "A Manual of the Genera of Beetles of America, North of Mexico," page 47, it becomes evident that there must have been some confusion in translating and rearranging Zimmerman's key (1919: 203–205). For example, the characters attributed in Bradley to *Agabinus* Crotch, are actually those of *Agabus* Leach (s. str.), while those for *Agabus* refer to the *Gaurodytes* Thomson of Zimmermann's paper. In addition, *Carrhydrus* Fall has been interpolated, although because of its unequal metatarsal claws it would have run to *Colymbetini* in the key to the subfamilies and tribes (page 45, couplet 10).

These facts suggest the need for another key to the genera of our *Agabini*, and the necessity of reconsidering the composition of this and allied tribes. Such a study is under way, but is not likely to be completed for some time; the following notes and key may be of use in the interim.

Tribe **Agabini** Sharp[3]

SHARP, 1882, Sci. Trans. Roy. Dublin Soc., (2) 2: 491.

Sharp separated the subfamily *Colymbetinae* into three tribes; the *Agabini* he distinguished by the linear group of ciliae at the posterior apical angle of the metafemora; the *Colymbetini* and a group of unassociated genera, lacking this group of ciliae, were separated by the fact that the genera of the former have sclerotised and transversely grooved

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[3]Actually Sharp proposed it as a "group," referring to names ending in *inae*, e. g., *Colymbetinae*, as tribes.

pleurites of the second abdominal segment. By this method, the genera *Hydrotrupes* Sharp, *Agabinus* Crotch, *Agabus* Leach, *Ilybiosoma* Crotch and *Ilybius* Erichson (and some others which do not occur in our fauna) were placed in the tribe *Agabini*, while *Scutopterus* Crotch, *Rantus* Stephens and *Colymbetes* Schellenberg went into *Colymbetini*.

Zimmermann (1919: 196) preferred the condition of the metatarsal claws as an ordinal character; the *Agabini*, with equal hind tarsal claws, thereby lost the genus *Ilybius*.

Unfortunately there are objections to both these systems. As Zimmermann pointed out, the metafemoral-cilia character practically fails in one section of the genus *Agabus* ("Subgenus" *Hydronebrius* Jakowlew, 1897). On the other hand his separation by the metatarsal claws also fails, for in the two species *Agabus erichsoni* Gemminger & Harold and *A. subtilis* Erichson, the claws are equal in the females, but appreciably unequal in the males.

It seems likely that the curious transverse rugae on the pleurites of the second abdominal segment may be of considerable phylogenetic importance. They lie between the dorsal ends of the second sternite and the corresponding spiracles, and are seen only by raising or removing the elytra; the pleurites of the following segments are never transversely rugose. Though the function of these rugae is enigmatic, they offer a clear-cut method of segregating the genera involved; they are either strongly defined—*Colymbetes*, *Rantus*, *Scutopterus*, and *Hoperius* Fall,—or completely absent—*Hydrotrupes*, *Agabinus*, *Agabus*, *Ilybius*, and *Carrhydrus* Fall. Elsewhere, they are known to occur only in *Dytiscus* Linnaeus and *Hyderodes* Hope, which two genera constitute the tribe Dytiscini; and very weakly in *Platambus* Thomson, a palaearctic genus included in the Agabini. Their occurrence in *Platambus* is puzzling, but since the species of this genus have certain other aberrant characters, careful study may suggest placement in another tribe.

Accordingly I am in favor of Sharp's system, especially when one considers that unequal metatarsal claws are found in a number of unassociated genera throughout the phylogeny of the Dytiscidae, for which reason they may be looked upon with suspicion as a tribal definition. There are two other points which argue strongly for placing *Ilybius* with *Agabus*, rather than with *Colymbetes*. F. Balfour-Browne (1934, 1935) has investigated the forms of the proventriculus in the Dytiscidae, and finds that on this basis, *Ilybius* is close to *Agabus* and allies; while Goodliffe (1939), studying the wing venation, shows clearly that *Ilybius* should be associated with *Agabus*. On habitus, both *Ilybius* and *Carrhydrus* are as strongly agabine as *Hoperius* is colymbetine.

KEY TO THE NEARCTIC GENERA OF AGABINI

Note.—The genera here included in the tribe Agabini will all run to couplet 10 (page 45) in Bradley, but will not remain together therein. They may be separated from the other tribes of Colymbetinae by the following combination of characters: metafemora with a linear group of ciliae near the posterior apical angles (figs. 11, 12); pleurites of second abdominal segment (elytra must be raised to see them) not strongly sclerotised, without transverse rugae; metatarsal claws equal or not.

1. Metacoxal processes in the form of rounded lobes (fig. 12).....2
   Metacoxal processes parallel-sided, lateral margins straight to the apices (fig. 11).....**Agabinus**
2. Metatarsal claws of equal length (fig. 12); if slightly unequal, then both are very short, only one-third length of fifth tarsal segment.....3
   Metatarsal claws obviously unequal, outer one of each pair two-thirds or less length of inner claw (fig. 10).....4
3. Labial palpi very short, terminal segments subquadrate (fig. 8)...**Hydrotrupes**
   Labial palpi approximately as long as maxillary palpi, terminal segments linear, not subquadrate (fig. 7).....**Agabus**
4. Labial palpi with penultimate segments enlarged, triangular in cross-section, the faces concave and unequal (fig. 9); genital valves of female dorso-ventrally flattened, not armed with teeth.....**Carrhydrus**
   Labial palpi with penultimate segments linear, not enlarged and triangular (fig. 7); genital valves of female laterally compressed and saw-like, with series of sharp teeth along upper edge.....**Ilybius**

Genus **Agabus** Leach

LEACH, 1817, Zool. Miscellany, 3: 68 and 72.

Type of the genus, *Dytiscus serricornis* Paykull, 1799; the only species cited by Leach.

This large Holarctic genus has had many of its species, or groups of them, removed as distinct genera or subgenera. The genus, *sensu lato*, is obviously composite and unwieldy, but a rather detailed study of the Nearctic and of many of the Palaearctic species has shown the interrelationships to be complicated; until a thorough revision can be made by someone having access to all the known species of both faunas, only inaccuracies can result from segregating our species under the names already proposed. In addition, there is the fact that many of the recently described forms have proved to be connecting links between groups of species previously considered as well defined and clearly separated from all others. This appears to be a general tendency; it has shown very clearly in Kinsey's studies on the species and genera of Cynipidae (1936), and has been commented upon by Saylor (1940: 61), quoting Arrow.

Accordingly, though cognizant of the names proposed at the expense of *Agabus*, the genus is here used in its broadest sense.

Key. The only recent key to our species is that by Fall, 1922. (See list of References at end of this paper). Many new species have been described since Fall's article.

Genus **Ilybiosoma** Crotch

CROTCH, 1873, Trans. American Ent. Soc., 4: 398 (in key), 413 (description).

Type of the genus, *Ilybius regularis* Leconte, 1852; designated by Crotch, 1873.

In his key, Crotch separated this genus from *Ilybius* by the equal metatarsal claws, from *Gaurodytes* of his paper by the lineal metasternal sidepieces, and from *Agabus* by the simple antennae of the males. In his discussion (p. 414) he made an obvious mistake, saying: "This genus differs from *Ilybius* by the sexual characters, and from *Agabus* by the narrow laciniae," when he meant *Agabus* and *Gaurodytes* respectively. Crotch included *Colymbetes bifarius* Kirby with a question mark, saying that it might represent a new genus, or belong in *Eriglenus* Thomson.

Regimbart (1878: 461) considered Crotch's genus to be a synonym of *Eriglenus* Thomson[4], but Sharp gave it standing in his monograph on the Dytiscidae (1882); it was not further disturbed until 1936, when Guignot, without further comment, placed it as a subgenus of *Agabus* in his key.

Recent studies have shown that it is quite impossible to separate *Ilybiosoma regularis* from a group of species in the genus *Agabus*, containing *lugens* Leconte, *seriatus* (Say), *brevicollis* Leconte, *ilybiiformis* (Zimmermann) and *minnesotensis* Wallis. The male genitalia of these species are remarkably similar[5]; and readily separable from those of our other *Agabus*. The narrow tongue-like metasternal wings[6] of *regularis*, considered to be diagnostic of the genus *Ilybiosoma*, are just as narrow in *minnesotensis*, slightly wider in *brevicollis* and *ilybiiformis*, wider still in *seriatus*, and broadest in *lugens* (figs. 1–6). Other important characters, such as the shapes of the prosternal processes and of the metalegs, the elytral sculpture, and the convexity of the body, show the same gradations from one extreme to the other in these species, suggesting that the series is a natural association.

Genus **Apator** Semenov

SEMENOV, 1899, Horae Soc. Ent. Russia, 32: 512.

Type of the genus, *Agabus kessleri* Hochhuth, 1871, (=*Colymbetes bifarius* Kirby, 1837, fide Zimmermann); designated by Semenov, 1899.

Semenov based the description of his genus *Apator* on *Agabus kessleri* Hochhuth, which he said is one of the most characteristic elements of the Central Russian water beetle fauna. He included Kirby's *Colymbetes bifarius*, though he had not then seen specimens of it; in relying on the description and figure given by Sharp (1882, p. 537 and fig. 170), he was misled as to the elytral sculpture, for Sharp's illustration is very poor; in fact it cannot compare with the one given by Kirby forty-five years earlier.

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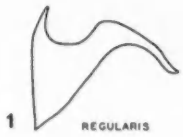
[4]Included in *Agabus s. lat.*, of the present paper.

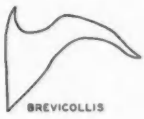
[5]*A. cordatus* (Leconte) and *bjorkmanae* Hatch are allied to the above species, especially to *seriatus*, on the basis of the male genitalia, as are also the species of the *guttatus* group of the Palaearctic fauna.

[6]The shape of the metatarsal wing has been used by some workers as a primary character on which to separate subgenera and even genera, at the expense of *Agabus s. lat.* Study of our species and of many from the Palaearctic fauna, has convinced me that the shape of the metasternum has varied independently a number of times in the history of the genus.

EXPLANATION OF PLATE I

Figs. 1 to 6. Right half of metasternum (ventral view) in each of six species of *Agabus*. (Drawn to the same scale.) Fig. 7. Labial palpus of *Agabus clavicornis* Sharp. Fig. 8. Labial palpus of *Hydrotrupes palpalis* Sharp. Fig. 9. Labial palpus of *Carrhydrus crassipes* Fall. (Figs. 7 to 9 are not drawn to the same scale.) Fig. 10. Apex of metatarsus of *Ilybius pleuriticus* Leconte, to show unequal claws. Setae omitted. Fig. 11. Ventral view of *Agabinus glabrellus* (Motschulsky) to show form of metacoxal lobes. Fig. 12. Same, of *Agabus punctulatus* Aubé. (Figs. 11 and 12 are drawn to the same scale. Tibial and tarsal setae are omitted.)

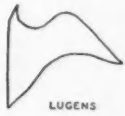

1
REGULARIS


2
BREVICOLLIS

3
SERIATUS

4
MINNESOTENSIS

5
ILYBIIFORMIS

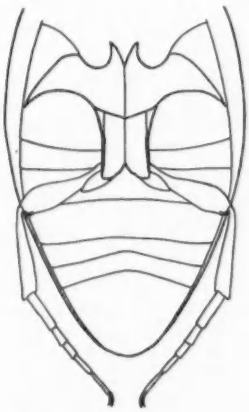

6
LUGENS

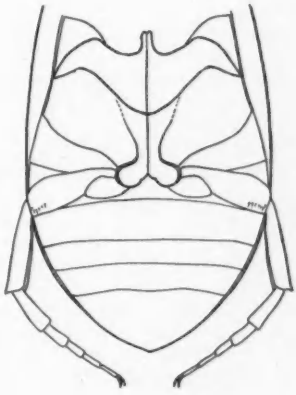
7
AGABUS

8
HYDROTRUPES

9
CARRHYDRUS

10
ILYBIUS


11
AGABINUS sp.


12
AGABUS sp.

Apator was given as a subgenus of *Gaurodytes*[7] by Zimmermann in 1919 (p. 204); as a distinct genus in his list of the Dytiscidae of the world (1920: 185); and again as a subgenus of *Gaurodytes* in 1934 (p. 149). In this last reference he gives *A. kessleri* (Hochhuth) as a synonym of *bifarius* (Kirby).

Semenov relied upon the following characters to separate *Apator* from *Agabus* and allied genera: (1) the aciculate elytral sculpture: in the basal two-thirds the elongate impressions are sub-oblique; in the posterior third, shorter and transverse; (2) the short, narrow, imperfectly-formed wings; (3) the tiny hairs, pointing straight downward, which arise from punctures along the face of the epipleurae, except in the basal third and near the elytral apices.

A careful examination of one hundred and fifty-six *bifarius*, all from Canada and the north-eastern United States, has shown that none of the above three characters will distinguish *Apator*. (1) The aciculate elytral sculpture may completely disappear; in a pair before me, from Marion, Massachusetts (Bowditch), the male is devoid of aciculate sculpture, while the female has a vague trace near the elytral apices. Such specimens are *Agabus*, clearly belonging to the association of species known as the genus or subgenus *Eriglenus* in European literature. (2) The wings are found to be dimorphic; irrespective of sex, almost exactly 45 per cent of the one hundred and fifty-six *bifarius* examined were found to have wings of normal size and shape; the remainder had short, narrow wings, and are apparently incapable of flight.[8] (3) The series of little eye-lash like hairs along the epipleurae are readily seen on clean specimens of *bifarius*; but they are equally apparent in the Palaearctic *Agabus labiatus* (Brahm), *undulatus* (Schrank), and *clavicornis* Sharp, in the Nearctic *hudsonicus* Leech, *versus* Brown, etc., and in *Carrhydrus crassipes* Fall.

For these reasons, *Apator* is here considered to be a synonym of *Eriglenus* Thomson.

Genus **Ilybius** Erichson

ERICHSON, 1832, Genera Dyticeorum, p. 18 (in synopsis of genera), and 34 (description).

Type of the genus, *Dytiscus fenestratus* Fabricius, 1781; designated by Westwood, 1838.

A genus of Holarctic distribution, but containing only about one-quarter as many species as *Agabus s. lat.*

The species of *Ilybius* are most readily separated from those of *Agabus* by their unequal metatarsal claws; however, as has already been mentioned, this is a sexual character in *A. erichsoni* and *A. subtilis*. An excellent difference between the two genera is found in the external female genitalia: in *Ilybius* the genital valves are laterally compressed and saw-like, with a series of sharp teeth along the upper edges; in *Agabus* the valves are never so armed. A pubescent area on the under side of each elytron, near the apex, was listed by Leconte and Horn

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[7]Included in *Agabus s. lat.* of the present paper.

[8]This subject is discussed and illustrated in the following paper.

(1883: 65) as typical of *Ilybius*, but it occurs also in *Carrhydrus* and in various species of *Agabus*.

Key. Excellent keys to both males and females of the Nearctic species have been published by Wallis, 1939.

Genus **Carrhydrus** Fall

FALL, 1922, Rev. N. Am. spp. *Agabus*, with . . . new genus . . . tribe Agabini, p. 35.

Type of the genus, *Carrhydrus crassipes* Fall, 1922, the only species known.

C. crassipes is one of the most interesting species of Dytiscidae in our fauna. In describing it from a single male specimen (collected at Edmonton, Alberta, by the late F. S. Carr), Fall considered that it should be placed next to *Ilybius*, and both included in the Agabini; with this I certainly agree. The unequal metatarsal claws appear to ally it with *Ilybius*, but the triangular and greatly enlarged penultimate segments of the labial palpi are at once diagnostic. In other attributes, especially the elytral sculpture, the male and female genitalia, and the male secondary sexual character, *Carrhydrus* is closely allied to the genus *Agabus s. str.*, i. e. to *A. serricornis* (Paykull), *clavicornis* Sharp, and *verus* Brown.

Genus **Agabinus** Crotch

CROTCH, 1873, Trans. Am. Ent. Soc., 4: 385 (in key), 397 (description).

In describing this genus, Crotch also erected for it the tribe Agabinini, no longer recognized.

Type of the genus, *Colymbetes glabrellus* Motschulsky, 1859; designated by Crotch, 1873.

Two small black species from the Pacific Coast are assigned to *Agabinus*.

Key. See Leech, 1941: Canadian Ent. 73 (3): 53.

Genus **Hydrotrupes** Sharp

SHARP, 1882, Sci. Trans. Roy. Dublin Soc., (2) 2: 491 (in key), 492 (description of type sp.).

Type of the genus, *Hydrotrupes palpalis* Sharp, 1882, the only species yet known.

Small black water beetles, found in streams in the Sierras of California. Length, 4 to 5 mm.

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THE NUMBERS OF ANTS IN ANT COLONIES

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The number of ants in an ant hill is a question of perennial interest. Forel's estimate of a maximum of half a million to a hill was not supported by Yung's actual enumerations (1900) which showed that of five hills of *Formica rufa* only one approximated one hundred thousand ants, the other four being well below that number. These lower figures were substantiated by the subsequent maximum enumerations of 2500 for a colony of *Camponotus pennsylvanicus* by Pricer (1908), of 8239 for one of *Formica exsectoides* by Andrews (1929), and of 12,358 for a nest of *Pogonomyrmex barbatus* by Wildermuth and Davis (1931). These and other like results led Bodenheimer (1937) to conclude that the populations of ant colonies vary, depending upon species and stages of development, from a few dozens to about a hundred thousand. This general statement has been supported by the counts of Pickles (1935, 1936) whose work was apparently unknown to Bodenheimer. Cory and Haviland (1938), however, subsequently described a nest of *Formica exsectoides* which they estimated to contain 238,510 ants (probably subject to a slight reduction according to Forbes (1938). This number more than doubles Bodenheimer's maximum limit but even it falls well below Forel's half million. In most of these contributions comment is made on the paucity of information of any kind in the literature on the size of populations in ant colonies. The following account contains an estimate of the number of immature individuals in an active nest of the dusky ant, *Formica fusca* Linn., that had been raided by the slave-making species *Formica sanguinea* Latr. I am indebted to Dr. Falconer Smith for the identification of these species and to Professor C. T. Brues for references to the literature.

The nest of the dusky ants under consideration was in a grassy open lawn and covered an area of about half a square meter. It had numerous apertures. The nest of the attacking red ants was also in open grassy land and distant some twenty meters from the nest of the invaded species. Between these two nests was a more or less direct trail a few centimeters wide over which the red ants were traveling rapidly in both directions. These ants when first noticed were in many instances seen to be carrying in their mandibles single dusky ants all of which were in process of transportation from the nest of the dusky colony

to that of the red one, for they were never seen being carried in the opposite direction. The dusky ants were evidently captured individuals that were being taken to their new habitation. Late in the afternoon of the first day on which this show attracted attention pale-covered individuals appeared among the transported population. On close examination these were seen to be larvae, pupae, or occasional callows. Like the transported adults these pale individuals were always being carried in the direction of the red ant nest. On close inspection they were found to be immature individuals of the dusky ant. At one place in the lawn the trail passed over a section of black garden hose which was so sunk in the sod that the ants were unable to pass under it and were of necessity obliged to climb over it. As the scattered procession marched over this hose it was very easy to count the ants that were carrying pale individuals because of the contrast in color of these individuals with the black hose. On the basis of these counts it was easy to determine the rate at which the immature dusky ants were being transported by the red ones.

The transportation of the pale individuals began in the late afternoon of the first day, about five o'clock, and lasted until eight o'clock that evening when with the oncoming of coolness the procession ceased. The trail was inspected during the night and no ants were seen at any time upon it. Presumably their operations stopped during the night. On the next day transportation of pale individuals began at about ten o'clock in the morning and lasted until near eight in the evening. During the second night there was again no sign of activity on the trail. On the third day transportation of pale ants occurred beginning in the morning and covering a period of about five hours. After that, though the red ants were still active, few or no pale individuals were seen to be transported. The total period of transportation for the three days thus amounted to about 18 hours. Over this period the rate of transportation was fairly uniform.

As the pale individuals were carried over the black hose they were counted for intervals of five minutes each. Twenty-one of these counts were made. They varied from 54 to 65 and averaged 59.4. Assuming this average to be reasonably correct as a sample of the eighteen hours it follows that the total number of immature ants transported by the red ants in that period must have been a little over 12,800. As the nest of the dusky ants was a disfigurement to the lawn where it was located it was dug up after the invasion of the red ants had ceased. The soil of this

nest was carefully examined and only 56 immature ants were found in it. This showed that most of the immature dusky ants had been removed by the raiders and left the general estimate of 12,800+ as essentially correct. The season of this exploit was the early part of August, 1941, and the nests of both species of ants seemed to be in full activity. It is fair to conclude then that a vigorous nest of *Formica fusca* may contain in midsummer some twelve to thirteen thousand immature individuals.

Although relatively few workers have recorded the total populations of ant colonies still fewer have had the opportunity of noting the numbers of classes in these populations. In fact the only detailed counts of this kind are those of Pickles (1936) who recorded the subpopulation numbers in the three species of ants whose nests were subjected to enumeration by him. In *Acanthomyops flavus* a nest of a total of 5613 individuals contained 959 immature ants. In one of *Myrmica ruginodis* with a total of 1534 individuals there were 249 pupae. And in a small nest of *Formica fusca*, the same species upon which the present report is based, of a total of 275 ants over a third or 102 were immature. These numbers are too scanty to allow of any reasonable comparisons. Nor does the number arrived at in this report have much general significance. It is but one additional enumeration which when added to other future counts may give a more detailed knowledge of the composition of ant colonies.

SUMMARY

An active, vigorous colony of the dusky ant, *Formica fusca* Linn., was closely estimated in August, on the basis of an invasion by the red ant, *Formica sanguinea* Latr., to contain from twelve to thirteen thousand immature individuals (larvae, pupae, and callows).

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NOTES ON THE BIONOMICS OF LIXUS FIMBRIOLATUS BOH.

(Coleoptera, Curculionidae)

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In 1889 Webster reported upon some of the habits of this snout beetle referring to it as *Lixus macer* Lec. The present paper, based on investigations carried out in the fall of 1939 and the spring and summer of 1940 at Urbana, Illinois, further contributes to the bionomics of this insect. The beetle was abundant along railroads, where the host plants grew profusely.

Emergence. The adults emerge from the pupal skins during the first three weeks of June. They remain several days or even weeks within the stems in which the larvae overwinter. Twenty adult beetles observed daily in the field remained within the stalks for an average period of six days before they attempted to escape. The exits were made through holes, 8 x 5 mm. in dimensions, gnawed in the side of the stems. Some of the beetles required several days to excavate the exit hole, others but a few hours. Some adults fail to make exit holes and die within the stems. Usually the beetles remain a day or two longer within the stems after constructing the exit holes. The majority emerge from the stalks during a three-week period beginning about the second week in June.

Feeding. Soon after emerging from their pupal chambers the adults begin to feed upon the edges of the leaves (Fig. 2, fi) of various composites. Webster (1889) observed both sexes feeding upon the foliage of *Helianthus*. In this locality, the sunflower, *Helianthus grosseserratus* Martens is eaten more than any other plant. Other plants upon which I found them feeding were Jerusalem artichoke, *H. tuberosus* L., common sunflower, *H. annuus* L., the sunflower, *H. scaberrimus* Ell., one of the rosinweeds, *Silphium integrifolium* Michx. and two species of goldenrod, *Solidago canadensis* L., and *S. altissima* L. The leaves of the cup plant, *Silphium perfoliatum* L., and prairie dock, *S. terebenthinaceum* Jacq. showed slight indications of having been eaten.

Oviposition. A period of several days, perhaps even a week or two, elapses between the time the adults emerge from the stems and the time egg-laying begins. During the egg-laying period pairs may be seen mating and *in situ*. The male rides around on the back of the female for

[1]This report represents a portion of the thesis which was submitted in partial fulfillment for the requirements of the degree of Master of Science in the Graduate School of the University of Illinois, 1941. The work was done under the direction of Dr. W. V. Balduf, Associate Professor of Entomology at the University of Illinois.

[2]Contribution No. 216 from the Entomological Laboratories of the University of Illinois.

periods exceeding an hour or more, mating with her during this interval. The female often continues eating on the edge of a leaf while copulating.

In 1872, Riley (1888) found that eggs had been deposited in maple-leaved goosefoot, *Chenopodium hybridum* L. and *Helianthus*. Coquillett (1883) observed females engaged in ovipositing in *Helianthus*. Webster (1889) also observed these beetles ovipositing in *Helianthus* and in *Silphium*. He considered it quite probable that they might oviposit in other similar plants. In this he was correct for I observed adult females oviposit in *Helianthus grosseserratus*, *Silphium integrifolium*, *Helianthus tuberosus*, *H. scaberrimus*, the cone flower, *Rudbeckia triloba* L., *Silphium terebinthinaceum*, *Solidago canadensis*, *S. altissima*, the petioles of the large basal leaves of *Silphium terebinthinaceum*, and the giant ragweed *Ambrosia trifida* L. The above plants are listed in order of preference. Other plants in which eggs were deposited are *Helianthus annuus*, *Silphium perfoliatum* and the common elder, *Sambucus canadensis* L. Many nest channels were found in the stems of waxy meadow rue, *Thalictrum revolutum* DC., which are hollow. I did not learn whether the insect actually oviposited or only prepared receptacles in the latter stem.

In the normal process of egg deposition, a female first places herself head downward upon the stem. Next she gouges out with her mandibles a narrow channel, by forward and backward movements of the rostrum. This channel is about a quarter of an inch in length, limited to the distance the female can reach without changing her position. It is not clean cut, but filled with matted fiber (fig. 1, mf). Remaining in the same position, she begins to excavate a burrow or egg-chamber slightly larger than the diameter of her rostrum directly into the pith. She brings her head out frequently to empty her pre-oral cavity of pith and frass. As she penetrates deeper into the stem she pushes her body away from the surface with her hind legs until she is almost in a horizontal position. Her recurved rostrum requires her to dig obliquely upward, rather than diametrically through the stem. As she progresses, her entire head is thrust within the stem to a point behind the eyes. When she has penetrated as far as she can reach she withdraws her head and makes a half-circle turn usually to the right so that her head is now directed upward. After inserting her abdomen into the egg-chamber she deposits an egg in the burrow. This is fastened with some adhesive substance to the wall of the chamber. The length of time required for this process is about fifty seconds. Following the deposition of this egg, the female executes a 180° turn to the right. Employing her rostrum she surrounds the egg with macerated pith and pushes it into place before deposition of the second egg which is likewise surrounded by pith in this manner (fig. 1, mp). After depositing the second egg, she fills the burrow with macerated pith by means of her mouth parts which are then used to pull the long matted fibers of the channel over the opening of the egg chamber. If more eggs are to be deposited the female backs up the stem slightly and gouges out another channel in which she constructs an egg chamber as before. The channel of this section of the nest connects with the first so that the two look as one (fig. 1). Although never observed, a second female might construct her nest adjoining that of another individual. The number of chambers composing the nests varied from one to ten.

Several variations from the normal egg-laying procedure were observed. One female was seen to construct the channel and egg-chambers while pointing upward upon the stalk causing the egg-chambers to point down the axis of the stem. Several nests of this nature were found. In a few instances females which did not have males *in situ*, as many did while ovipositing, swung their abdomens back and forth transversely, pendulum fashion, over the entrance of the chamber just before inserting an egg. In two such cases the swinging of the body continued for fifteen seconds.

Perhaps the paramount factor which determines the number of egg-chambers a female will construct for a given nest is a condition within the insect itself, namely the number of mature eggs present within its ovaries when excavating the nest. The primary external factor appears to be the toughness of the plant fibers in which the nest is being constructed. During the first half of July, when the plants are relatively young and tender, the majority of the nests are constructed in the basal portion of the stems. At this time there is a higher percentage of many-chambered nests in these regions than will be found a month later when the fibers in the basal portions tend to become tough and woody. During the last weeks of August the many-chambered nests are to be found in the upper extremities of the plants where the fibers are less woody, also the percentage of one- and two-chambered nests will have increased in the basal portion. These conditions suggests that the females become fatigued more easily when constructing nests in tough stalks and do not excavate many-chambered nests in them.

The location of the nests in the stems of *Rudbeckia triloba* and *Silphium integrifolium* would seem to indicate that the surface covering of the stem and the kind and arrangement of the leaves play an indirect part in determining the size of the nests. The former plant stem is quite hairy which apparently prevents the insect from climbing to any great distance up the stalk. In the case of the latter plant the leaves are opposite, sessile and chordate. Barriers are thus formed by the leaves which tend to prohibit the insect from advancing to the upper extremities where the fibers are less tough. The majority of the nests constructed in these two plants, therefore, are composed of but one or two chambers since they are limited to the basal regions where the fibers are more woody.

The most common number of egg-chambers to a nest is one, two being next most frequent (fig. 1), three next, and so forth to ten. Of 150 chambers examined 99 or 66 per cent contained two eggs per chamber, 36 or 24 per cent one egg per chamber while 15 or 10 per cent lacked eggs entirely.

Duration of Egg Laying and Egg Stage. The egg stage (fig. 3) was found to have a duration of from six to seven days. Eggs were discovered from June 26 to September 21, which indicate that the egg laying period extends from the latter part of June until the middle of September. Each female probably oviposits many times during that period. It is also probable that those excavating nests with one or two egg-chambers construct a larger number of nests than do those excavating many-chambered nests.

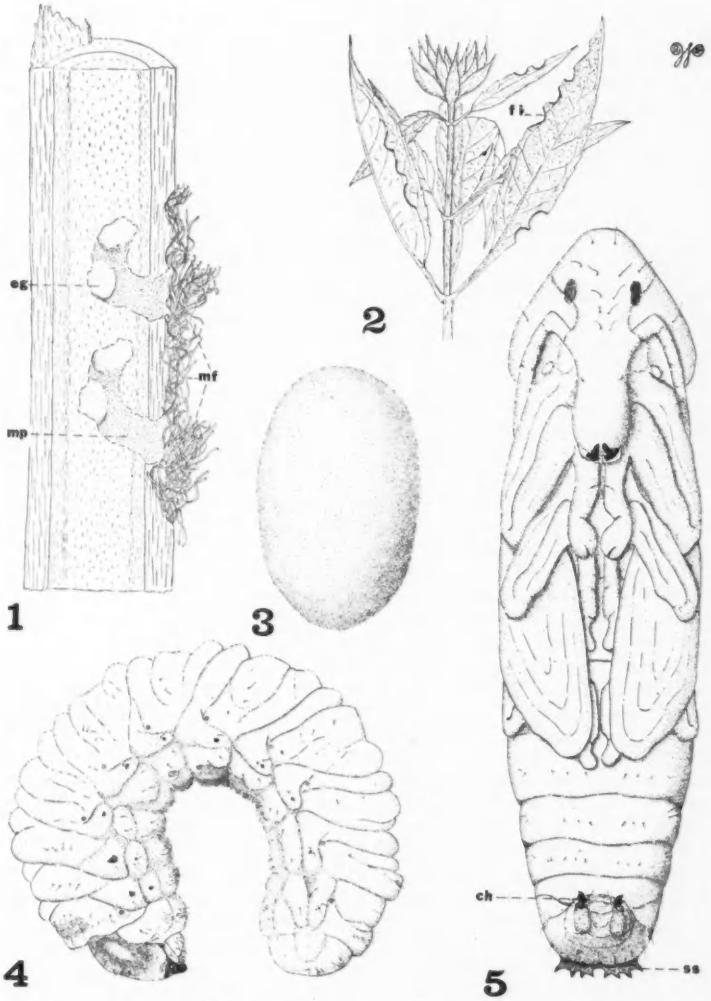

FIG. 1. Longitudinal section of a *Helianthus* stem showing position of eggs of *Lixus fimbriolatus:* eg—egg; mp—macerated pith; mf—matted fibers. 2. Injury to *Helianthus* leaves by feeding of adult weevils. fi—feeding injury. 3. Egg of *Lixus fimbriolatus*. 4. Larva of *Lixus fimbriolatus*. 5. Pupa of *Lixus fimbriolatus:* ch—caudal hooks; ss—spines.

Hostile Factors. Instead of hatching, some eggs turn black, decrease in size, and gradually disintegrate. Some of those deposited later in the season are destroyed by larvae of their own species. While eating their way up the stem these larvae crush or puncture the later-laid eggs with their sharp mandibles as they pass. Other coleopterous larvae may possibly destroy the eggs incidentally as do the *Lixus* larvae themselves. Several nests were found to contain larvae and pupae of a species of *Eurytoma*. This is a genus of the chalcidoid family Eurytomidae, order Hymenoptera. Although many adults of this hymenopteron were seen throughout the summer running about wildly over *Lixus* nests and annoying ovipositing females of this beetle, never were any seen to oviposit. Where its larvae or pupae were found within a nest no *Lixus* eggs were present. In a few cases, punctured *Lixus* eggs were found beside the eurytomid larvae. However, there were indications that the larvae eat the pith of the stem, hence the *Lixus* eggs may be destroyed by the wasp quite by chance. Further observations on the relation of *Eurytoma* to *Lixus* are needed.

Season of Larvae. The larvae of *Lixus* grow and develop during the summer months and pass the winter in the fully developed larval condition within the stems of the various host plants. Larvae may be found about eleven months of the year. It is probable that any given individual spends nearly ten months in the larval stage.

Larval Habits and Development. Upon hatching the larvae begin feeding on the pith of the stems in which the eggs were deposited, boring upwards towards the top of the plants. As they ascend they leave a passage packed with frass, and may proceed up the stalks to distances varying from two inches to three feet. Eventually, however, they turn around and eat downward for a distance of two to ten inches. Subsequently they again turn around and eat upward the same distance. Such upward and downward movements in the stem continue throughout the summer. By the second week in September, when the larvae become fully developed (fig. 4), each has excavated a chamber in which to pass the winter. These chambers vary in length among the different individuals, depending upon the distance the larvae had bored. In one instance the entire development of a larva took place in a section of stem two inches long, i. e., the larva was always within two inches of the nest where it hatched from the egg.

Webster (1889) expressed the belief that the larvae are not cannibalistic. However, I found evidence that they might be, especially in the early part of their development when they are eating their way up the stems. This evidence was provided by checking the number of larvae found within 50 stalks with the number of individuals one would expect to find, assuming all eggs hatched and all larvae lived. Investigations showed there were 68 per cent less larvae than one would expect to find. In my opinion not more than 20 per cent of the eggs were destroyed in the manners previously mentioned. I concluded, therefore, that some of the remaining 48 per cent must have been destroyed by other members of their own species, because of a cannibalistic tendency which may have developed from too crowded conditions.

After the larvae have reached maturity some of them girdle the stems from within during the last week in September and the first

weeks of October. The process of girdling is performed with the mandibles, which scrape at the wall of the chamber while the insect is headed downward. Scraping begins at one point on a circle and continues around until the entire circumference has been girdled. The frass from this process is not eaten but fills the chambers about the larvae. Upon completing the girdle the larva tucks its head ventrally under the rest of the body and by many peristaltic contortions finally reverses its position so that its head points upward. It then pushes its way through the loose frass, which fills the lower portion of the chamber, by scooping and pushing it back under itself with head and thorax. After passing through the frass, a larva packs this material down so that a compact plug is formed. The wind easily breaks off the stalks at the point of girdling. The girdled sections may be found lying about on the ground or loosely attached to the main stalks during the late fall and winter. Stems were observed in which two girdles, about one-half inch apart, had been made by the same larva. Just why some larvae should girdle the stems completely while others do not even begin to do so is not known.

Larval Instars. I collected larvae in different stages of development during the summer in an effort to determine the number of larval instars. The length of the larvae and the width of the head capsules were measured. It was soon found that Dyar's law would not apply to this insect, for small larvae which appeared to be of an early instar often had larger head capsules than much larger larvae which were apparently of a later instar. Neither does Przibram's rule appear to apply to this species, for according to it the larvae undergoes fourteen molts. While this number is by no means impossible, it seems improbable in view of the fact that other beetles whose instars are known do not molt as many times.

Arrested Development. An effort was made to determine whether the arrested development of the larva during the winter is a true diapause, occurring irrespective of environment, or is only a direct response to environmental conditions. From a series of experiments it was found that individuals whose growth had become arrested during subfreezing weather continued their development when exposed to warmer temperatures. Although the effective temperatures were not determined it was noted that development took place about twice as fast at 80° F. as at 70° F. and much faster at 70° F. than at 60° F. At a constant temperature of 80° F. a humidity of 29 per cent was sufficiently low to kill 15 per cent of the larvae, while all individuals subjected to the same temperatures but to a humidity of 80 per cent lived. However, larvae exposed to the low humidity developed as rapidly as those exposed to the high humidity with the exception of the few that died. Even the latter individuals developed as rapidly as the others prior to their death. *Lixus fimbriolatus*, therefore, is homodynamic, i. e., development continues as long as temperature and humidity are favorable.

Before pupation in the spring, approximately 50 per cent of the larvae gnaw a small longitudinal slit, about 5 x 0.5 mm. in dimensions in the wall of their chambers. The presence of the slits make it very easy to find stems which contain pupae or larvae about to pupate.

I observed, from reared insects, that there is a very distinct change in the movements of the larvae prior to pupation. Instead of the slow,

even, undulant motion, the larvae take on the quick, jerky, whip-like motion of the pupae a day or two before the last larval skin is molted.

The larvae transform to pupae in the spring. I found the first pupa on May 4. Judging from its dark color it had been in this stage for several days. The last pupa was found on June 16. Adults emerge after a duration of 21 to 24 days in the pupal stage.

In most insects the pupal stage is considered an inactive one. However, the pupa of *Lixus fimbriolatus* is very active. It is able to move rapidly up and down the interior of the stem with the aid of two caudal hooks and several rows of sharp abdominal spines. (fig. 5, ch, ss).

Enemies of the Pupa. Not infrequently the pupae fall prey to ants which enter their chambers through the small slits in the side of the stalks made by the larvae before pupating, or through open ends of the stems.

SUMMARY

1. There is one generation a year.

2. The adult, upon emerging from the pupal skin, remains within the stem several days before making an exit hole, and usually a few more days before actually departing from its cell.

3. In this area of their distribution, the adults begin to emerge from the stems of the various composites and other plants, in which the larvae overwinter, during the first or second week in June.

4. The adults feed and mate until mid-September upon many of the plants in which they oviposit.

5. Egg laying takes place from the last week in June until about the third week in September.

6. Nests are composed of egg chambers ranging from one to ten in number.

7. The eggs, of which there are usually two per chamber, hatch in six or seven days and the larvae begin to feed upon the pith of the stems becoming full grown after the middle of September.

8. During the first and second week in October many of the larvae girdle the stems from within.

9. *Lixus fimbriolatus* is a homodynamic insect.

10. Pupation first occurs within the stems about the first of May and lasts until about the middle of June.

11. From 21 to 24 days of the life of the insect are spent in the pupal stage.

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